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Miniature Circulating Systems for Small Laboratory Aquaria

C. M. BREDER, JR.

The American Museum of Natural History, New York 24, N. Y.

(Plates I & II; Text-figures 1-5)

INTRODUCTION

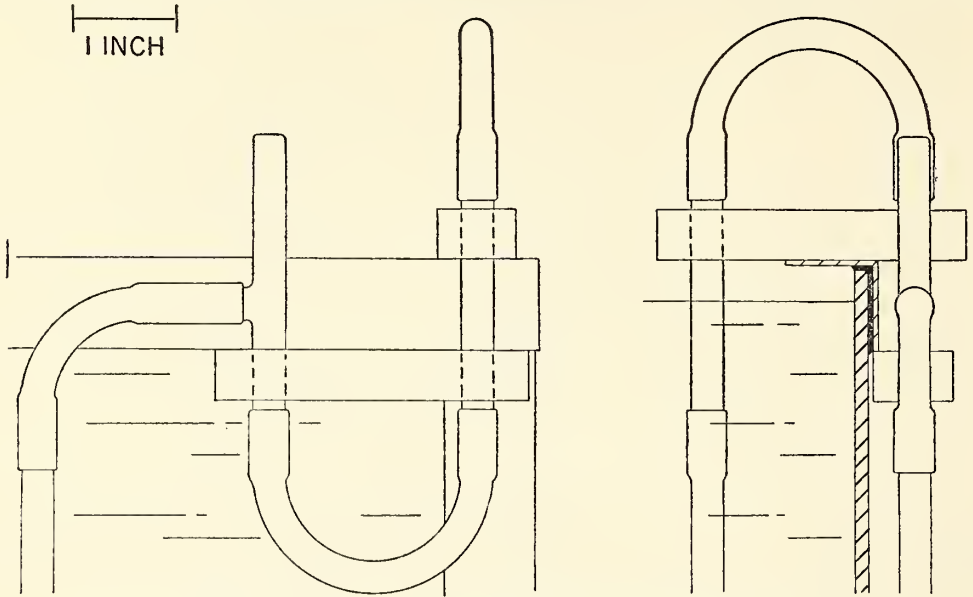
BECAUSE of the requirements of certain experiments it became necessary to establish various small, but fully controllable circulating systems in small aquaria. These have included both open and closed freshwater systems and closed saltwater systems. As the designs eventually worked out have proved to be entirely satisfactory, and as many colleagues have inquired about these systems, with a view to building similar ones for their own purposes, the details of construction and operation are explained here.

Primarily these systems are the outgrowth of work of earlier years at the old New York Aquarium where much larger, but similar, equipment formed the basis of operations. This equipment itself had been developed from schemes used by older institutions of similar kind. Naturally, many persons had a hand in developing the arrangements and devices employed at the New York Aquarium. For these reasons the origins of the devices were not always clear, but those chiefly interested and responsible for them at the Aquarium were C. W. Coates and the late C. H. Townsend, and H. Knowles. Townsend (1928) and Breder & Howley (1931) reported on some of these features. It has been found that by suitable modification of the principles of the larger devices it is possible to develop very useful miniature equipment. Such need, of course, applies only to laboratories not connected with large public aquariums and which consequently lack the utilities usually only to be found in such places. These devices have been worked out in connection with experimental work carried on in the laboratories of the Department of Fishes and Aquatic Biology of the American Museum of Natural History, which has been supported in part by the National Science Foundation.

OPEN SYSTEMS

An "open system" as here used refers to one in which the water is used but once and not recirculated. That is, there is only a supply line and a drain line. This calls for little comment in present connections except where a very small, well-regulated flow is required. Such apparatus may be arranged to provide as little as a specified number of drops a minute, and will maintain a surprising accuracy if properly designed.

The overflow provided for this system is a constant-level syphon. If such a syphon is made by a glass blower it is expensive, subject to breakage and is not readily cleaned. Syphons can be quickly and cheaply made of some straight glass tubing, a tee, some flexible rubber or plastic tubing, and two small pieces of wood or plastic strip. No dimensions are given, as these will vary with the individual needs, although Text-fig. 1 is drawn to scale. The two pieces of plastic are identical and should have two holes drilled in them that will snugly fit the glass tubing. These parts are then assembled to make a constant-level syphon attached to the lip of an aquarium as shown in Text-fig. 1 and Pl. I, Fig. 1. The lower piece of plastic may be fastened to the aquarium by small clamps or be cemented to it. The open, upper end of the tee vents the syphon. If a cap or plug is placed on this it immediately becomes a simple syphon and will drain the aquarium to the level of its inlet tube. This is sometimes found to be an added handy feature. The level of the water in the aquarium will be that at which the overflow water spills out through the horizontal leg of the tee. Adjustments of this to a fine point may be made by raising or lowering the tee through the hole in the plastic support, or this whole external assembly may be moved up or down by altering the position of the straight length of tubing which passes through the hole in the other piece of plastic connecting it with the tube in-

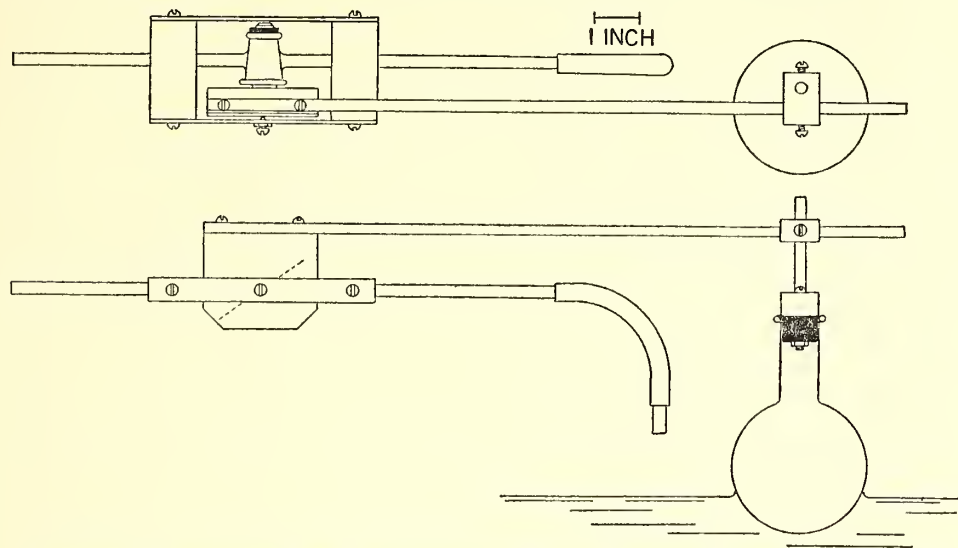


TEXT-FIG. 1. Side and end view of constant-level syphon made up of standard parts.

side the aquarium. By arranging the outside part of the syphon to lie along the aquarium wall, as shown, the danger of its being in the way of operations is reduced. It is obvious that cleaning presents no problem with this type of syphon. In most cases a plastic or glass strainer is placed over the intake end of the syphon. If something does nevertheless block the syphon tube from the aquarium, it almost always can be cleared by blowing into the open end of the tee and restarting the syphon by drawing on this same open end of the tee while the outlet tube is held shut. It is possible and sometimes more convenient to attach the outer portion of the constant-level syphon to a small board which is affixed to a pivot at its upper end so that it is free to rotate on the stationary part attached to the aquarium frame. A small handle pointing upward from there makes its adjustment simple and marks on the latter in reference to some stationary part make return to a former rate of flow exactly possible. The action is simply that by rotating the part of the syphon so that the horizontal part of the tee raises or lowers, the level in the aquarium follows accordingly. This in turn affects the float valve, which is described below. The rate of flow will increase if the syphon outlet is lowered and decrease if it is raised. This is useful where the exact level of water is not of any importance but where it is desired to vary the amount of water flowing through the aquarium by specific amounts and where it is necessary to repeat such changes in flow at will.

If the water supply has considerable pressure, such as is ordinarily encountered in city water systems, or approaches it, a pressure-reducing valve which may be regulated should be employed. This can bring the pressure down to a value which will not burst or otherwise destroy the light equipment to be employed. This valve placed someplace in the supply line should be set so as to deliver little more than the maximum amount of water which will be required of it. Another way to accomplish the same purpose is to permit the supply water to run into a small reservoir of no more than sufficient height to provide enough head of pressure. Into this reservoir the supply water is allowed to run continually, of a little more volume than the aquaria will ever need. This is necessary to maintain a constant head in the reservoir. A small excess will overflow and go to waste by this method. It is economic only where water saving has no significance.

The water flowing into this aquarium is controlled by a float-valve constructed of a glass stop-cock, a suitable-sized chemical flask and some small parts of either wood or plastic. These are assembled as shown in Text-fig. 2 and held together by iron screws and two pieces of strip steel. This metal is mentioned because of the danger of toxic salts forming if brass were used, since such corrosion might fall into the aquarium. A one-hole cork is bolted to a piece of lucite and then inserted into the mouth of the flask as shown. A dowel or plastic rod is inserted in the other hole in the plastic piece and secured.



TEXT-FIG. 2. Top and side view of float-valve for control of inflow of water and additives.

A similar piece of plastic is movably secured on this rod and on a similar one at right angles to it, extending from the valve. This is so arranged that the center of the flask comes to rest directly below the horizontal rod extending from the valve. This is best seen in the plan view of the device. By loosening the two set screws in the upper plastic piece the flask may be moved vertically on the one and horizontally on the other. Pl. I, Fig. 2, shows one arrangement of this device.

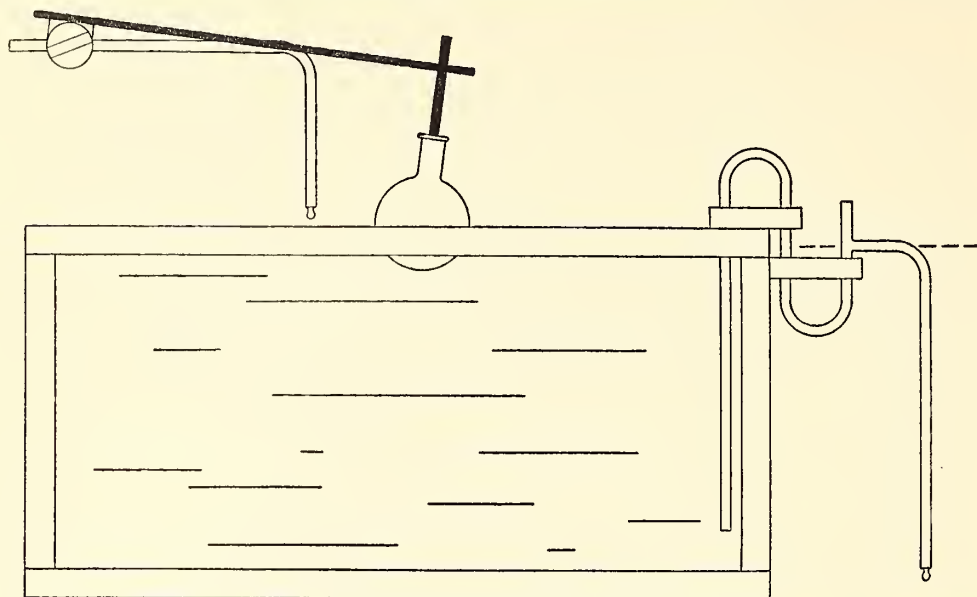
The extending glass tubes which are an integral part of the stop-cock are inserted through two snug holes in the wood or plastic end-pieces of the valve and these are held in position by the two steel strips which are held in place by four wood screws. In the center of one of these steel pieces a hole is tapped into which is screwed a set screw with a pointed end (about 60°) and a lock nut as shown. The stem handle of the stop-cock is imbedded in a piece of wood cut about as shown. For this purpose a suitable space is hollowed out in the block into which the stem is inserted, the space around being filled with plastic wood or similar product. The face of the block and the stop-cock stem must be at right angles. On the outer face of the block a small steel strip is affixed with a small drill-tip impression at its center on the axis of the stem. Into this the pointed set screw fits as shown. This is adjusted so that the valve works freely without being too tight or leaking. This prevents the glass stop-cock from working loose and leaking after a time of long-continued operation. The diagonal dotted line on the block indicates the position of the hole through the plug as well

as that of the handle on the stem. It is shown in a position just fully closed. It is obvious that with a fall in the water level the valve will open proportionally to the change in water level and shut itself off as the water level rises.

The interaction between the constant-level syphon and this valve is indicated in Text-fig. 3. It is clear that danger from flooding could come only from some damage to the equipment. If, for instance, something clogs the overflow in any way, the float valve shuts itself off when it has reached whatever predetermined point for which it has been set.

As an extreme point of precaution a safety alarm or shut-off could be built as an entirely separate system. Such a device, which has never failed so far as the writer's experience goes, consisted of an old pair of contacts such as are to be found on relays to one member of which was fastened a shell vial. This hung over the water in such a manner that when the water rose over a specified place it lifted the vial and pushed the two contacts together. It operated on two dry cells to ring a doorbell but could be used with a relay to switch on house current to operate any suitable device. This could be a normally open solenoid valve placed in the supply line. Such extreme caution would only be warranted where a little flooding would be disastrous.

It is obvious that this float-valve could be used under certain experimental procedures to add chemicals to an aquarium at a prescribed rate by inactivating the float and fixing the rate of flow by hand. It also could be used to bring the concentration of some chemical to a fixed limit and then hold it at that point in flowing water



TEXT-FIG. 3. Diagram of interaction between float-valve and constant-level syphon. Dashed line represents level of water in aquarium and syphon arm.

aquaria. The water supply would operate as above described and a second float-valve regulated to add much less chemical than the water flow would move with it and act as a follower to the other if there was any fluctuation in the flow of water, thus holding the additive in proportion to the change of water. Also a single float could be arranged to operate the two valves in proportion to the setting of each.

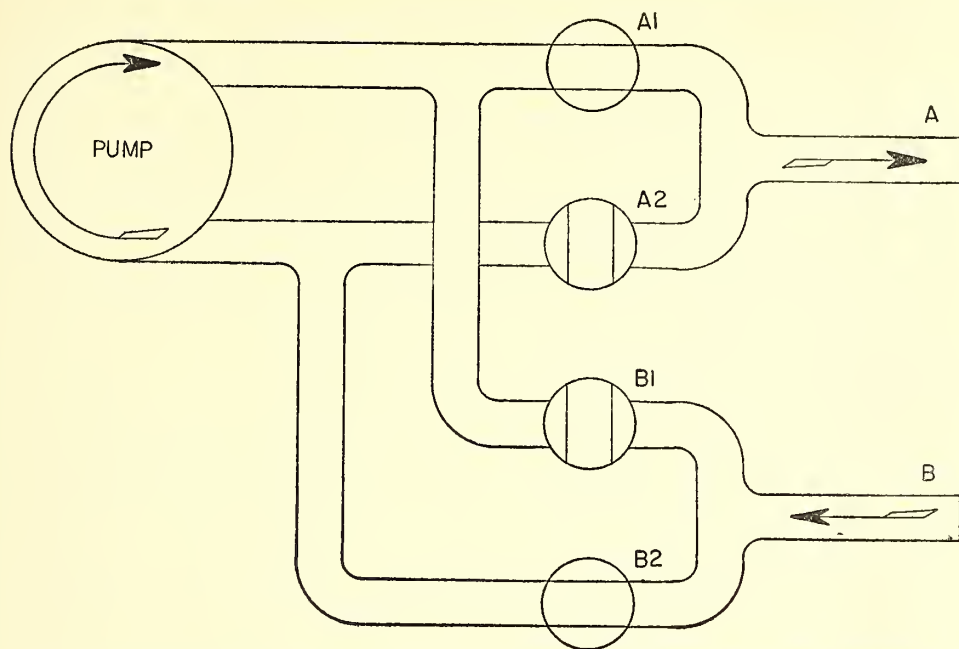
While the designs of these float-valves have varied from time to time, all have been built embodying the same principles as herein described. The first and somewhat primitive one has, at this writing, been in service continually for more than four years and is still entirely satisfactory and dependable.

CLOSED SYSTEMS

The term "closed systems" refers to circulating systems in which the water is returned to the aquaria after filtration or other treatment and none is allowed to run to waste during normal operations. Some such system is mandatory for the maintenance of marine forms remote from a ready supply of sea water, and often convenient or necessary for various experimental procedures involving freshwater aquaria. This is especially true of cases where it is necessary to maintain close control of some feature such as temperature, chemical quantities and the like. By use of such means it is possible to maintain a series of aquaria with absolutely identical water conditions, as the water in all is part of a

common body. Consequently no matter what transpires in one aquarium there is no opportunity for the water of that one to depart from the characteristics of the rest since it is moving freely from one aquarium to the other and is being continually and effectively mixed.

An especially useful arrangement for some purposes is one in which the flow between aquaria may be continuously varied from maximum in one direction through zero flow to maximum flow in the opposite direction. This may be readily accomplished by the adjustment of four valves while the pump runs continuously in one direction at constant speed. The details of the arrangement of these valves are shown diagrammatically in Text-fig. 4. Pl. II, Fig. 3, is a photograph of such a device. In operation the action is as follows. With valves A2 and B1 closed and the others open, the flow is out through pipe A and returns through pipe B, as indicated by the arrows, at maximum flow. If these valves are reversed so that A1 and B2 are closed and the others open, the flow through pipes A and B is reversed, although the flow through the pump remains as indicated by the arrow on it. To pass uniformly from the first position, as shown in Text-fig. 4, through a state of no flow to the reverse, either valve A2 or B1 can be gradually opened. This reduces the speed of water movement because of "back leakage." After one of them has been opened fully the opening of the other can further retard flow. When it, too, has been fully opened, that is with



TEXT-FIG. 4. Diagram of piping and valves for continuously variable flow from maximum in one direction through zero flow to maximum in the opposite direction.

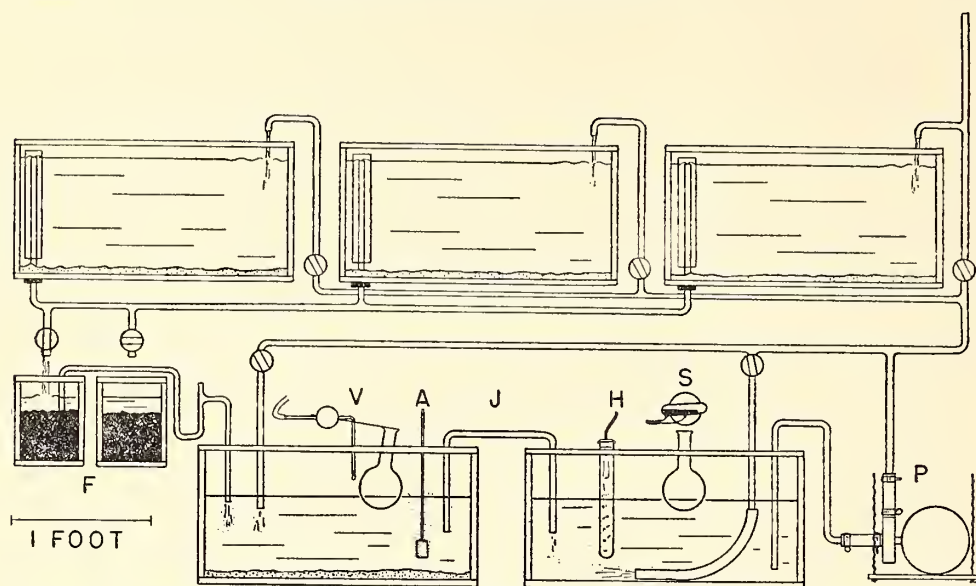
all valves fully open, there should be no flow through pipes A and B, as there is as much pump pressure in one branch of both A and B pipes as in the other. Then by beginning to close either valve A1 or B2 the flow begins to move in the opposite direction. When these two are fully closed, the maximum flow in the opposite direction has been reached.

If three valves are arranged on either line A or B or such a set on both, various water treatment devices may be placed in the series, such as a heating or cooling device, in which case the water may be best passed through a glass coil for heat exchange purposes. This arrangement could equally well be used for any kind of decontamination which might be required or for the introduction of specified materials being mixed with the passing water. Unlike most aquaria plumbing, in this case the water must pass from one aquarium to another, so that as many as may be needed can be placed in series.

A diagram of a more usual arrangement for a closed circulating system is shown in Text-fig. 5. This is the form which is perhaps most useful for general laboratory purposes. Here each aquarium is respectively supplied and drained directly from a common supply and return. It is advisable to use a pump of somewhat greater capacity than needed for the purpose. With this means the excess water can be returned to the reservoir without passing through the aquaria,

which greatly assists in the efficient application of whatever water treatment is being given and insures adequate pressure for the system. Simple filters may be made by wedging a piece of glass in a small aquarium and filling the intake side with suitable filter material, while the reservoir may be used for whatever chemical or other treatment is to be applied. Two may be provided, as shown in the figure, and used alternately or together. A constant-level syphon takes the water to the first reservoir aquarium. Only one syphon is shown, which may be switched to the other aquarium for cleaning purposes.

The pipes and fittings used in this system are standard hard rubber. Connections between aquaria at the same level may be made by "jumpers" which are preferably of hard rubber. Their use is indicated in the lower level aquaria shown in Text-fig. 5. These have been found to be fully satisfactory and in several years' operation have not clogged nor have they become airbound. They are, however, not suitable for the overflow lines of the upper series of aquaria. Here constant-level syphons may be used as shown in Pl. I, Fig. 1, or, preferably, a hole may be drilled in the slate bottom of each aquarium and a one-hole rubber stopper holding a glass tube inserted. Still better is the installation of a hard rubber standpipe locked in place with fittings. The drilling of slate is not easily accomplished and there is considerable danger of



TEXT-FIG. 5. Diagram of arrangement of a closed circulating system suitable for small marine aquaria. A = aeration outlet. F = filters. H = heater and thermostat. J = jumper. P = pump on hanging support. S = safety cut-off switch. V = float-valve. Distilled water supply carboy not shown.

cracking or otherwise damaging the aquarium. The manufacturers will supply aquaria with such holes drilled on order.

Since the supply to the aquaria of this system is preferably from the top, as indicated, the drain line as above described may be made to draw water from the bottom of an aquarium by the following simple means. A tube of glass, or other material, of larger diameter than the drain tube and as long as the depth of water in the aquarium, is placed over it, reaching nearly to the bottom of the aquarium. Since the larger tube extends above the surface, water leaving the aquarium must enter the annular space between the two tubes and pass up between them to spill into the open upper end of the inner tube. In addition to giving the aquarium a better circulation, much detritus is drawn up through this arrangement and delivered automatically to the filters. The outer tube, if of glass, may be positioned by slipping a short piece of plastic tubing on its lower end and cutting various openings or notches in the plastic. The area of these passages should of course be at least equal to the cross-section area of the inner tube. The annular space between the inner and outer tubes should also have this much area, at least. On the other hand, it is best not to make the annular space much larger than needed because this will cause the water flowing through it to move with less speed. The value of this arrangement as a detritus remover is thus lessened, for the slower-flowing

water will not lift as heavy particles as will the faster.

As such a system is usually intended to be operated continuously for long periods without attention, a safety feature may be built in which would shut down the pump if the water in the reservoir rose too high or fell too low. The one in current use, shown in Pl. II, Fig. 4, was improvised from the tube of a mercury switch. This was mounted on a rotatable glass shaft running through a support of plastic. It was actuated by a chemical flask float by means of a thread over a small drum so that the motion of the float was transmitted to the pump switch. Any unusual change in the water level, either positive or negative, would indicate some radical failure at some point in the system. Since the aquaria which held the fish were drained by an overflow they would continue to hold their water level so that stopping the pump would insure the retention of water there. Even if one of the aquaria leaked and lost its contents the others would not suffer by draining through the system to it because of this protective device.

To prevent normal evaporation from stopping the pump, a supply was provided which operated in conjunction with the protective switch. This supply was administered by a float valve identical with that shown in Text-fig. 2. A very nice adjustment was found possible with these two float-actuated mechanisms, so that the dripping from the float-valve supply became

directly proportional to the evaporation, without at any time tripping the protective cut-off float-valve. On very humid days it could be seen that the number of drops per minute was notably less than on a clear dry day when evaporation was high. In the case of saltwater aquaria this device had an added important application which is discussed under the treatment of salt water.

Because of the nature of the controlling devices above described, it is necessary to observe certain details in starting the system. The levels of water in the lower series of aquaria will be different when the pump is not running than when it is in operation. This is mostly because the drain lines of the upper series of aquaria empty themselves into the lower aquaria when the pump is stopped. Therefore the water is carried at a lower level in these aquaria so that there will be no overflowing when the circulation has been stopped. For this reason a switch should be shunted around the cut-off float to be used in starting the system before the operating level is reached. It will not suffice to wedge the float into a position where its switch will be closed, because its free action is necessary to establish its proper level of operation. After a dynamic equilibrium has been achieved by adjusting both the cut-off device and the density control device, the shunt switch should be opened, after which the system should control itself. If it does not at first, very obvious adjustments of either or both will bring them into the proper relationships.

The diagram of the closed marine circulating system shown in Text-fig. 5 employed seven aquaria for holding experimental fishes, only three of which are shown in the illustration. Three "reservoir" aquaria were used, of which only two are shown. These were standard commercial aquaria measuring $2' \times 1' \times 1'$. The two smaller, used as filters measured $10'' \times 8'' \times 6''$. The pump was driven by a 1/10 hp motor and was rated at 10.8 gals. per min. at zero head. The pipe sizes are not indicated, as they would naturally vary with the needs of each system. In this one the flow was slow but sufficient at about three gals. per hour through each of the seven top row aquaria. At the right of Text-fig. 5 the supply pipe is extended upwards for some distance and with the upper end open. This permits building up whatever head of water is desired without subjecting the pipe to pressure greater than that produced by gravity.

Although the upper series of aquaria were intended for holding fishes and the lower series were regarded as treating reservoirs, the latter

too may be, and have been, used to hold fishes, that is, all but the one from which the pump draws water, since the suction and turbulence here would be destructive to most small fishes. Aerating stones and a standard aquarium glass heater and thermostat comprised the rest of the water-treating equipment. The heater which turned off when the water reached 74°F . was sufficient to keep the water throughout the system close to that temperature as it was only slightly higher than the normal room temperature. It was found that the aerating stones made it possible to permit the flow of water in the lower aquaria to run through submerged pipe outlets and thereby reduce the amount of splashing and consequent salt deposits. This was not found necessary in the upper series, for each supply pipe carried only one-seventh of the flow in the lower pipes.

MATERIALS

It is strongly recommended for all the purposes for which these devices were developed that only hard rubber or some biologically inert plastic be used. In fresh water, iron plumbing is adequate for many purposes but for sea water no metals whatever should be used if any degree of satisfaction is to be obtained. Hard rubber and acrylic resin or vinyl chloride-acetate copolymer plastics have been used throughout for those parts which come in contact with the water, including the pumps.¹ Also it is important to see that no brass or other such metals are used in positions over the aquaria in order to prevent possible corrosion falling into the water.

In all cases involving the use of pumps for aquarium purposes it is best to have a spare stand-by duplicate pump and motor unit as a precaution against the failure of either motor or pump. It is then possible to change such a unit in a few minutes, in the case of accident, with no serious interruption to the operation of the system. It is most convenient to use flexible connectors between the pump and the rigid plumbing leading to the aquaria. It is then only necessary to unfasten two screw clamps and insert the new unit in place. This type of arrangement is shown in Pl. II, Fig. 3.

An additional advantage of this kind of connection is that it dampens any vibrations, from the pump or motor, which tend to travel throughout the system along rigid connectors. The pump in Pl. II, Fig. 3, was suspended by

¹In the systems described, the plastics used in the construction of the apparatus go under the trade names of Lucite and Plexiglas and the tubing under the name Tygon. The pumps have been supplied, complete with motors, by Broadbent-Johnston, Inc., Compton, California.

four light cords, a means which is also very effective in quieting such small machines.

TREATMENT OF WATER

The treatment of fresh water for aquarium purposes is too well known to warrant comment in present connections and is usually necessary only under special situations. The maintenance of sea water in a satisfactory condition is quite another matter, however. It is not the purpose here to discuss the theoretical aspects of the chemical and physical conditions of sea water. Such matters may be found extensively treated by Sverdrup, Johnson & Fleming (1942) and Harvey (1955). The following is intended purely as a guide for the practical application of principles which have been found adequate to maintain a variety of marine fishes. Under this treatment regular reproductive behavior was quickly established in both *Histrio* and *Bathygobius*, which had been reared from juveniles. It also permitted a variety of volunteer algae and microorganisms to establish themselves. Incidentally these aquaria were kept under conditions of no daylight, the illumination being supplied by fluorescent tubes of the "warm white" type necessary for satisfactory plant growth. The periods of light and darkness were controlled by a time switch.

The equipment found necessary for the control of sea water consisted of a small hydrometer, a colorimetric pH device and some simple titrating equipment.

The filters were provided with bone charcoal and the bottoms of the aquaria and reservoirs were floored with so-called coral sand, and aerating stones were placed in various convenient places, but not in the aquaria containing fishes.

The specific gravity and pH were taken every day until the rate of change was established and from then on were taken at less frequent intervals. This rate of change will vary with the quantity of water, the bulk of the organisms contained and the temperature of the water. At less frequent intervals titrations were made to determine the variously-called excess base, titration alkalinity, or alkaline reserve. This method, which measures the bound CO_2 , is not especially accurate but is sufficient for the present purposes. It consists of titrating a sample with N/100 hydrochloric acid to which brom-cresol purple has been added as an indicator. After the purple color has vanished the sample is repeatedly boiled and further titrated until the purple color no longer reappears on heating. If the sample consists of 100 cc. to which five drops of indicator have been added, the final burette reading in cc. multiplied by 0.1 gives the bound

CO_2 or bicarbonate in millimols/liter. This method is not to be generally recommended for accurate work but is sufficient as a comparative measure of how far and how fast the aging water is departing from its original value.

With this information, corrective measures may be taken. The specific gravity is nearly taken care of by automatic means involving the use of the float-valve already discussed. Under normal operations distilled water is used to make up for the evaporation of sea water, which of course tends to increase its density thereby. This has been satisfactorily supplied from a five-gallon carboy on a shelf higher than the float-valve. The operation of the float-valve holds the amount of water in the system at a constant volume, which means also that the dissolved salts will remain at a constant amount. If it is desired to increase the density of the water, instead of using distilled water as an additive, sea water may be used until the specific gravity has reached the desired level. If it is desirable to reduce the salinity, water may be withdrawn from the system while distilled water is used in the float-valve supply. This may be conveniently accomplished by means of a syphon with a small hose clamp so that the flow is restricted to a drip slow enough to permit the float-valve to follow. Although distilled water was customarily used, in its absence tap water was used with no detectable effect on the fishes or the system.

If the pH falls to lower values it may mean that there is an increase in the amount of free CO_2 present. This could indicate too many organisms for the volume and temperature of the water or too much decomposition for the anti-acid components of the system to dispose of rapidly. The calcium carbonate in the sand should react with the acids formed and unless there is overcrowding this type of decreasing alkalinity usually does not present a problem. If the placing of fresh activated bone charcoal in the filter results in an abrupt increase in the pH, it is almost certain that there is too much free CO_2 present. The use of charcoal renewed at short intervals will bring the CO_2 content down but the charcoal rapidly becomes saturated and cannot be thought of as a regular part of the regulatory process. An increase in the number of aeration stones or amount of air they pass, while much slower in its effects, is a much more satisfactory way to insure against the accumulation of CO_2 .

If on a falling pH, none of the procedures above mentioned increase the pH significantly, the titration reading should be carefully checked and it too should show a decrease. This would indicate a lowering of the bound CO_2 which does

not normally occur in an unoverloaded system in the presence of calcareous sand. If it does, however, more sand may be added, or sodium bicarbonate may be dissolved and administered with the distilled water through the float-valve. Since the sand alone tends in a long-term sense to disproportionately increase the Ca in solution as compared with the Na, the occasional use of sodium bicarbonate, which tends to do the reverse, aids in keeping these two quantities in more nearly normal proportions. See Breder & Smith (1932).

The described procedures may seem to be somewhat complicated, but they are, in fact, not much more complex than those involved in maintaining a similar number of standing fresh-water aquaria. After the equipment is built and regulated, so that valves and controls are in balance, there is nothing to be done with them at any time and in fact there should be no tampering with them at all. It is probably wise to post warnings to this effect. There is little aquarium cleaning to be done, as most of the accumulating detritus is automatically deposited in the filters. Aside from feeding the fishes and sometimes cleaning algae off the glass sides, the latter being controlled by adjusting the lighting arrangements, there are the following routine matters to be done. These will vary with each installation but may be approximated by the regimen under which the described installation of seven aquaria were controlled, as follows.

Read pH and Sp. G	Twice a week	5 min.
Titrate sample	Once a week or less	15 min.
Fill distilled water carboy	Twice a week	5 min.
Clean filters	Once in 2 weeks	15 min.
Make adjustments based on above information	Once a month or longer	Various

The need for changing the pump and motor is such a rare occurrence as not to figure in the above schedule and should not take more than 5 minutes. Every attempt has been made to reduce the maintenance of the system to its minimum. It is not uncommon for the system to be left alone for as long as three days, as over a long week end. The only thing to normally expect at the end of this period is some extra-hungry fishes. It should be borne in mind that the smaller the system—that is, its total amount of water—the more rapidly decomposition or contamination can spread through it. It is prudent not to reduce the size of the equipment more than necessary.

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EXPLANATION OF THE PLATES

PLATE I

- FIG. 1. A constant-level syphon in operation.
- FIG. 2. Float-valve for the control of inflow. Note: This is the arrangement as used in the closed saltwater system. The placement is for convenience, but usually valves are placed close to one end.

PLATE II

- FIG. 3. Pump provided with reversible flow device. The plastic pump here shown is powered by a 1/80 hp motor and is rated to deliver 3.7 gals. per min. at zero head.
- FIG. 4. Safety control for closed circulation. Its relation to the system is indicated in Text-fig. 5. The pipes at the extreme right are the pump intake and excess return.

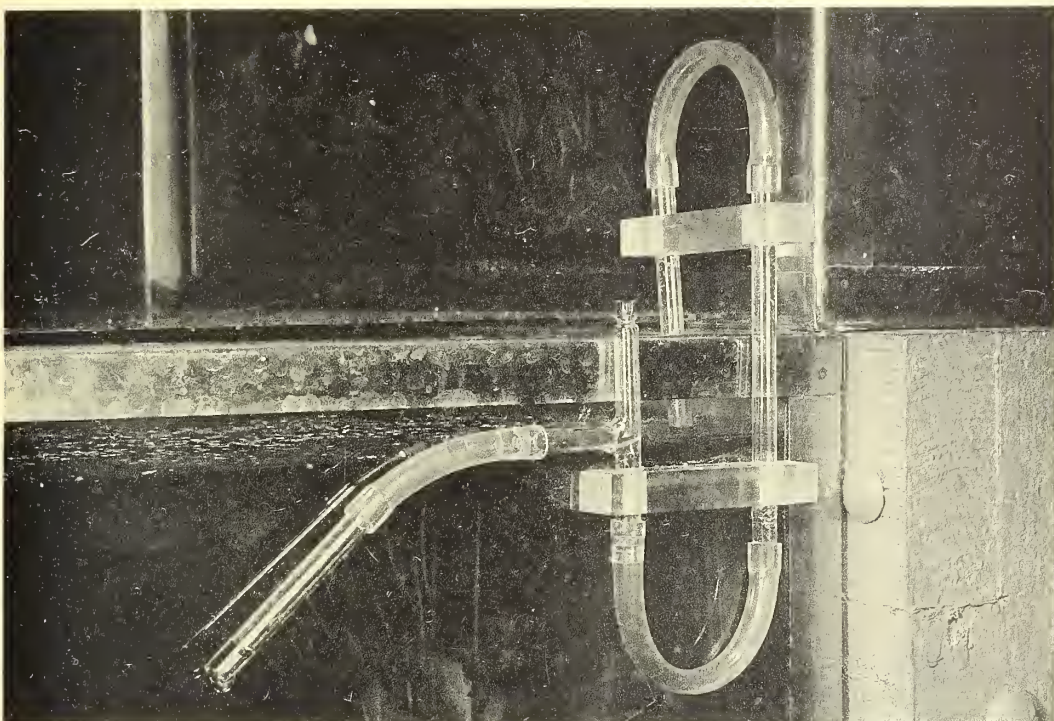


FIG. 1

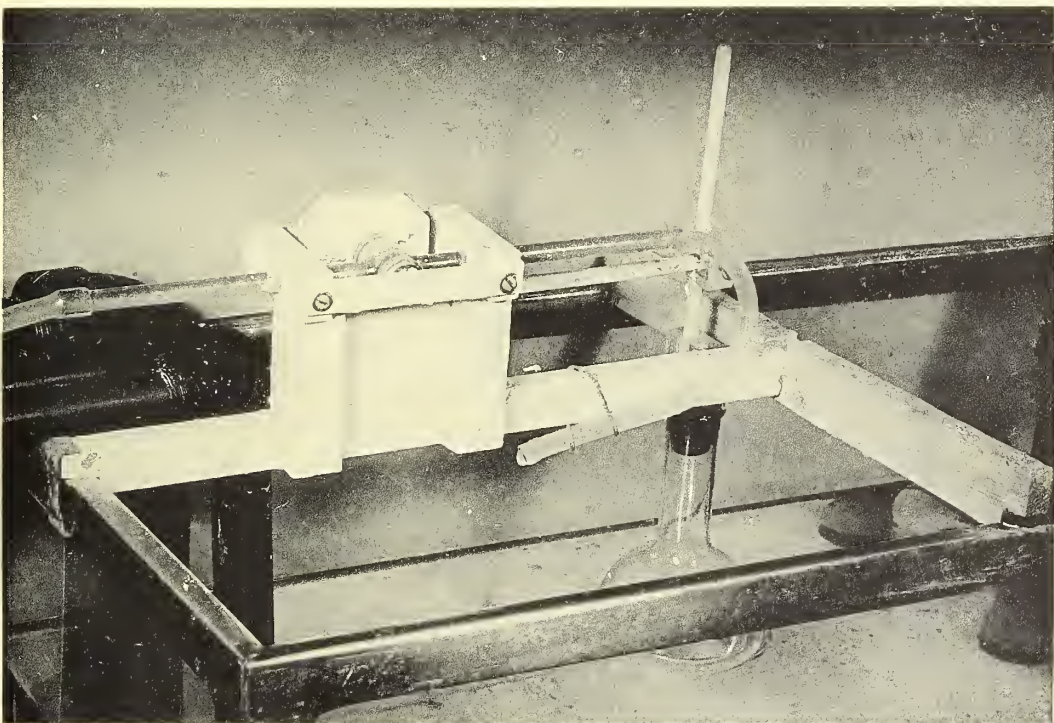


FIG. 2

MINIATURE CIRCULATING SYSTEMS FOR SMALL LABORATORY AQUARIA

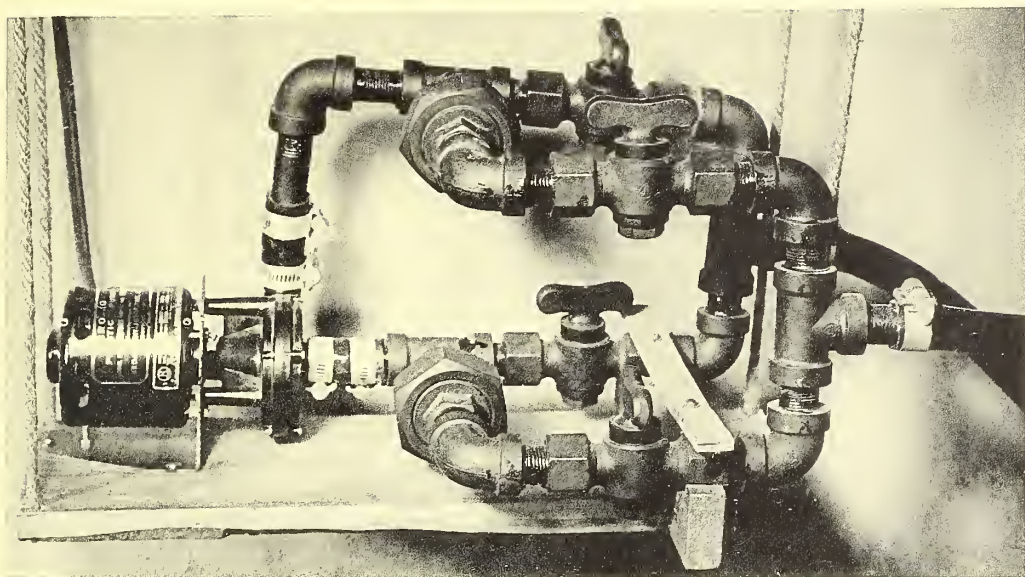


FIG. 3

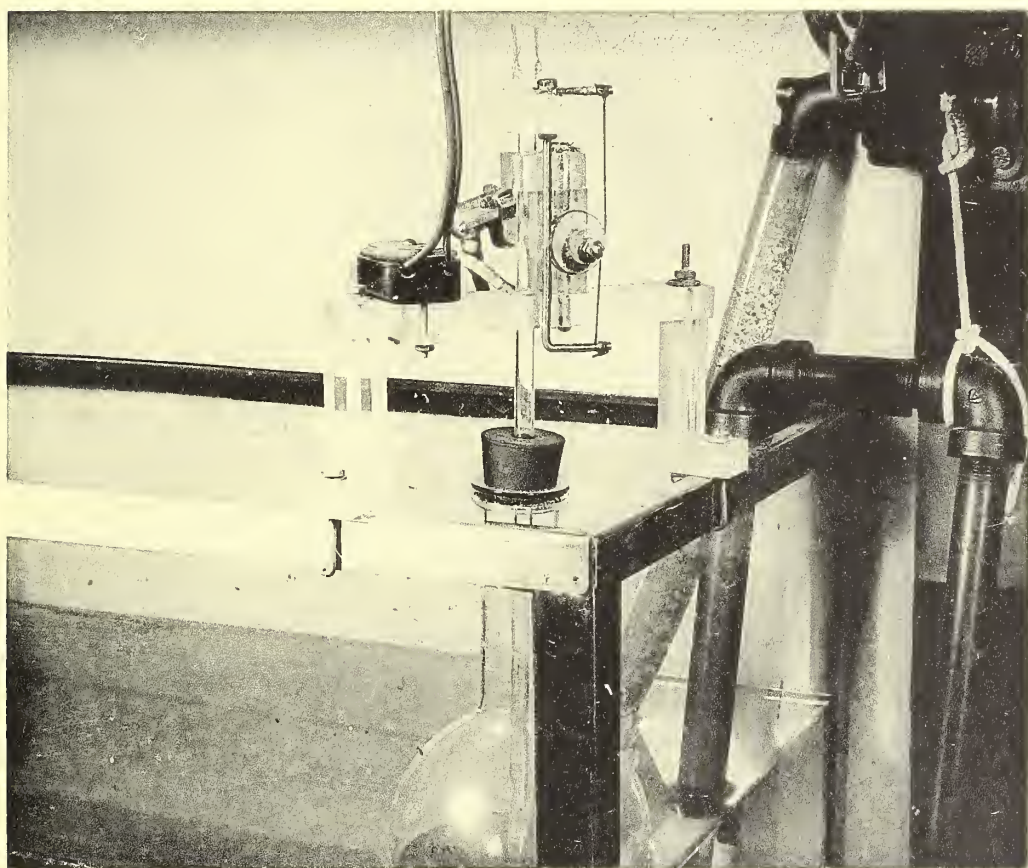


FIG. 4

MINIATURE CIRCULATING SYSTEMS FOR SMALL LABORATORY AQUARIA

2

The Behavior of the Bottle-nosed Dolphin (*Tursiops truncatus*): Mating, pregnancy, parturition and mother-infant behavior¹

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(Plates I-III; Text-figure 1)

INTRODUCTION

BECAUSE Cetacea bear their young in water, data on the normal progress of pregnancy and parturition, together with information on mating behavior and post-natal development, have been either lacking or only incompletely available to biologists interested in these animals. The greatest part of the information as yet recorded has been received from whalers and other sea-faring men who have observed these animals in the open sea, where conditions are far from ideal for such observations (Lütken, 1888; Pedersen, 1931; Slijper, 1936). James (1914) first observed the birth of a Common Porpoise (*Phocaena phocaena* (Linnaeus)) in captivity in the Brighton Aquarium, but this was a stillbirth. Khvatov (1938) and Sleptzov (1940) both observed what they believed to be normal births in the Common Dolphin (*Delphinus delphis* Linnaeus) in shallow portions of the Black Sea, or in large seines in which a number of animals were confined prior to being drawn toward shore. McBride & Hebb (1948) and McBride & Kritzler (1951) were the first, however, to record their observations under conditions almost ideal for this purpose.

In their 1951 paper, McBride & Kritzler pub-

lished on this subject the latest data taken at Marine Studios, Marineland, Florida, where the activities of the Bottle-nosed Dolphin (*Tursiops truncatus* Montagu) in a 75-foot circular tank may be viewed conveniently through portholes set in the walls. At that time five pregnancies resulting in normal births had been under observation. Three animals had conceived in the tank. Since then five additional pregnancies, all resulting in normal births, have been observed, providing many additional data. The present report is based upon a series of observations instituted by one of us which was conducted over a period of slightly more than three years, and which for the last year and a half was on a daily basis. During parts of the latter portions of these observations, both authors were able to be at Marineland at the same time, and observations could be made almost constantly, so that a steady daily record was kept which provided the observers with continuous data, not only on the group as a whole but also on the activities of any individual animal.

Up to the time of the 1951 paper by McBride & Kritzler, new animals were introduced at irregular intervals and some deletions were made in order to keep the population at a desirable level and at the same time to minimize the possibilities of combat which resulted on a previous occasion in injuries to a newborn dolphin (McBride & Kritzler, 1951). Since then, the colony has become a stabilized and self-perpetuating group, in which the only additions are those by birth. This fact has enabled the observers to obtain data on the growth and maturation of several individuals. One of the females born in the tank has reached the beginning of her eighth

¹The authors wish to extend their thanks to the staff of the Marineland Research Laboratory, Marineland, Florida, for their cooperation and for the use of their facilities and equipment. They also wish to express their appreciation to Dr. Lester Aronson of the American Museum of Natural History, Mr. F. G. Wood, Jr., of the Marineland Research Laboratory, and Dr. Frank A. Beach of the Department of Psychology, Yale University, for their special help in reading the manuscript.

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year and terminated her first pregnancy in March, 1954.³

Table 1 shows the names, sexes, dates of birth and relationships of the members of the stable population of the tank. In addition, Happy, a fully-grown adult male, and presumably the father of all the infants conceived in the tank, was present throughout the three years covered by the present data. Frank and Floyd, born in the tank, were removed in December, 1953.

actively sought the company of the selected female by such stratagems as chasing her when she left him, hovering over her when she hunted for fish or was otherwise occupied in one spot, and by returning to her immediately after both had been engaged in other activities, such as feeding. Such exclusive companionship lasted from three or four days to several weeks.

This period of prolonged companionship often, but not always, led to further activities on

TABLE 1. STABLE POPULATION OF *Tursiops truncatus* IN TANK AT MARINE STUDIOS.

Date of Birth	Sex of Infant	Name of Infant	Name of Mother	Duration of Birth*	Remarks
Feb. 26, 1947	Female	Spray†	Mona	28	
April 23, 1948	Male		Mrs. Jones	21	Died of injuries
May 8, 1949	Male	Algiet†	Susie	117	
May 12, 1950	Male	Frank	Pudgy		
May 15, 1950	Male	Floyd	Mrs. Jones		
Feb. 7, 1953	Female	Mamie	Mona		Died June 13, 1953
Feb. 23, 1953	Female	Maggie	Mrs. Jones		
Feb. 27, 1953	Female	Nellie	Susie		
May 7, 1953	Male	Mitch	Pudgy	68	Died Feb. 22, 1954
March 4, 1954	Female	Peggy	Spray	48	Died March 19, 1954

*Duration of birth of infant in minutes, from first appearance to complete emergence. Where no figure appears, the birth took place at night and was unobserved.

†These animals were conceived in the wild before the capture of the mother. All other infants in the table were conceived in the tank.

PRECOPULATORY BEHAVIOR

In the spring of 1952, 1953 and 1954 (February to May inclusive), there occurred a number of special activities which appeared to be the preliminaries to copulation, since the copulatory pattern was frequently seen to follow them. The aggregate of these activities over a period of time between two animals of opposite sex we term courtship. It should be understood that not all of these activities need necessarily take place between any two particular animals, and further, that they need not follow any particular order.

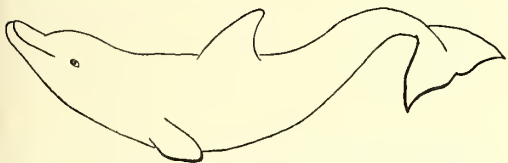
During the major portion of the year the adult male changed his companions often, swimming with one animal for a few minutes or a few hours, and rarely remaining with it for more than a few days. His companions during this time were other males, females or young animals of either sex. He also remained alone for long periods. During the early spring, however, he showed preference for the company of one particular female and remained with her for prolonged periods. He either accepted the presence of other animals or avoided them, but he

the part of the male, depending on the attendant circumstances. At times, without any further activity, the male suddenly broke off the partnership and shifted his attention to other interests, and there was no further association between the male and female for weeks or months. On the other hand, he often suddenly increased his attention to her and engaged in activities which were more aggressive and more directly associated with precopulatory behavior. These activities were quite varied and included posturing, stroking, rubbing, nuzzling, mouth-ing, jaw clapping and yelping. Any or all of these were included in any sequence and varied in intensity, becoming most intense just before exhibition of the copulatory pattern.

Posturing. — Although this type of act appeared at any time during precopulatory behavior, it was usually one of the first indications, aside from prolonged companionship, that precopulatory activities were about to become more intense. The male swam toward the female and took up a position in front of her, or slightly to one side, but well within her line of vision. He then bent his body in such a way that from the side it took on the shape of an S-curve, head pointing up, flukes down, as in Text-fig. 1. He maintained this position for about two to five seconds, and then resumed normal swimming.

³This paper was submitted for publication on February 13, 1956.

The action was repeated immediately, after several minutes, or not at all, depending on the female's general responsiveness and the other activities taking place in the tank. All males postured sometimes, but males were seen to begin courtship without posturing. Therefore it appears to be a subordinate portion of the precopulatory pattern of behavior. Although posturing was usually shown by the male, it was observed in the female under certain circumstances which will be described later.



TEXT-FIG. 1. Male dolphin in posturing position.

Stroking. — During normal swimming the male took up a position just behind and below the female. When this happened, the female often altered the normal motion of her flukes in such a way as to stroke or lightly pat the head of the male as she swam. At times the positions were reversed, and the male stroked the female's head. The stroking motion was easily distinguished from the normal swimming motion, and also from the lashing of the flukes given by another animal in an attempt to avoid contact or to get away. Such action on the part of the two animals was usually assumed when they were resting, and was the least vigorous and energetic of the sexual activities. At other times either male or female swam in such a way as to bring one or both flippers in contact with some part of the other's body (Pl. I, Fig. 1), and by swimming along or across the other's body produced a stroking effect. Another form of the same activity took place when one of the animals turned on its back and, swimming beneath the other in the same direction and at the same speed, moved its flippers rhythmically back and forth across the other's body. The other member of the couple responded by repeating the action at the same time so that the two sets of flippers stroked each other. Such actions could, of course, be continued only until it was necessary for one or the other to rise to breathe, but it was resumed immediately following this, and with interruptions for respiration was sometimes continued for half an hour or more. Stroking was also carried out by gentle movements of the head against the body of the partner. Another variation took place when one animal placed itself beside or beneath the other,

and stroked the genital area of the partner with the tip of one fluke.

Rubbing. — This was a much more strenuous action in which one member, usually the male, swimming at a fast pace, advanced upon the female and rubbed part of his body vigorously against hers (Pl. I, Fig. 2). This advance took place from any direction relative to the two animals, but was most dramatic when the male approached the female head on, as if to engage in a head-on collision, and then turned aside at the right moment and just enough to produce vigorous contact of the two bodies along their lengths. This type of inter-animal contact rarely lasted for more than a few minutes, during which the male made repeated rushes at the female. Trumpeting and whistling sounds were sometimes heard during this time. The female sometimes turned after each rush and swam toward the male as he repeated the maneuver, enhancing the vigor of each contact, or she rushed away, leaping out of the water in a real or apparent attempt to escape. When the latter took place, the male usually rushed to the spot where she was to reenter the water and rubbed energetically against her as she did so. (Pl. I, Fig. 3).

Nuzzling. — Nuzzling took place when one animal applied its closed snout to some part of the body of the partner and moved it around in that area. Although this action took place in a number of other situations, such as the nuzzling which goes on between mother and infant, the male often nuzzled at the genital area of the female, possibly as an investigative measure, and also possibly stimulating her thereby. The female, at times, nuzzled the male in the same way.

Mouthing. — (Pl. I, Fig. 4) Mouthing was an activity similar to nuzzling, but took place with the mouth open. Although used during precopulatory activity in the same manner as nuzzling, it also took place in other ways. When in an appropriate position, one animal took a flipper, fluke or sometimes even the head or snout of the partner between the teeth (Pl. I, Fig. 4), and gently closed the mouth upon it, thereby holding the part. This grasp was a gentle one, and was released as the partner pulled away, without leaving tooth marks or gashes. This is in contrast to the grips taken on each other by two fighting males, which result in deep cuts and gashes inflicted by the sharp teeth. Either nuzzling or mouthing of the male's genital region by the female sometimes resulted in an erection.

Jaw Clapping. — At times during the companionship of the male and female, a second

male interfered in the relationship between them, either by swimming between the two, separating them, or by nuzzling the female while she swam with the first male. In such a case, the male's response was rapid and often violent. He is able, by clapping his jaws together forcefully, to produce a sharp loud sound, which can be heard at a distance of fifteen feet or more from the outer wall of the tank. As early as 1940, McBride recognized this sound as "the principal form of intimidation" when produced by a dominant animal. Often jaw clapping was sufficient to discourage the intruder, but if not, the first male resorted to violent lashes with his flukes, sometimes throwing the offender against the side of the tank with tremendous force; or he actively attacked the intruder with his teeth, inflicting serious gashes upon the other's flukes, flippers, back and head. Jaw clapping was also used if the female swam away for a short time, or if another female interfered. In these cases, however, the final results were rarely violent, since the partner rejoined the male immediately, and an interfering female hastily left. In other situations, jaw clapping was used by non-dominant animals as a sign of displeasure and not necessarily as intimidation.

Yelping. — During the more intense stages of precopulatory behavior, another sound, characteristic of this situation, was often heard in the tank. This sound has been interpreted to be a type of mating call (Essapian, 1953; Wood, 1953). It was a high-pitched yelp, delivered as a series of short sharp cries. The number of yelps in a series varied from two or three to seven or eight, and the series might be repeated after an interval of about fifteen seconds, or might not be repeated for a much longer interval, depending upon the circumstances. There can be no doubt that the male produced these sounds, since when he was in the proper position relative to the observer, the flap of the blowhole and the area behind the blowhole could be seen to move as if they were being depressed at the time that the sound was heard. No bubbles escaped from the blowhole with the production of this sound. The male yelped very rarely when he and the female were swimming quietly together. On the other hand, if the female strayed away from his vicinity, or stopped to investigate another animal or an object in the tank, in the majority of cases the male promptly produced a series of the yelping cries and continued to do so at short intervals until the female returned to him. If she did not respond at once, he continued to yelp until she did. Immediately upon her return to him the yelping ceased. If another female responded, she was

ignored. Since, as far as the investigators could determine, yelping was heard only during the mating season, and the selected female responded, it is felt that the interpretation of this sound as a mating call is valid.

Although the male consistently swam with a single female during the earliest days of the spring season, the most intense of the precopulatory activities did not take place at this time. Such activities seemed to begin shortly after the birth of the first infant of the year, and evidence is accumulating that true precopulatory activity may be triggered by this birth. In 1953, the first infant was born on February 7, and the first display of intense sexual activity on the part of the male, accompanied by yelping, was seen three days later. Since no observations were taken on the two previous days, it may have taken place even earlier. In 1954 the first infant was born on March 4, and the beginning of yelping and intense sexual aggressiveness on the part of the male began the same afternoon. Since the March date is quite late in the year for the appearance of the first infant, and continuous observations were carried out through all of February, it can be seen that there was a possible connection between the two events. However, more evidence is necessary to establish a clear relationship between them.

The pattern of the male's sexual activities previous to copulation was not a consistent one. Any or all of the actions described above were involved, and any or all of them could take place within an hour or two. On one day the male engaged in each of them and periods of intense activity alternated with periods when the two animals swam quietly together for an hour or more. On another day he persistently engaged in one of them, rubbing for instance, though the entire day, and displayed none of the others, resting only a few minutes at a time before resuming his activity.

Initiation of precopulatory behavior by the female.—The part of the female in a paired situation was less energetic than that of the male. When she was the chosen companion, it was only rarely that she engaged in any but the mildest of precopulatory activities toward him. She swam close to him, perhaps maintaining contact with him by an extended flipper touching his body, and she was occasionally seen to initiate mild stroking activity. She actively cooperated with him, however, when he initiated the more intense actions, and there was one occasion when she actively took the lead. As mentioned above, during the height of the rubbing activity on the part of the male, she often

rushed away from him at great speed, and leaped far out of the water, perhaps to escape his attentions. On such occasions, he sometimes joined her in her leaps, but more often he swam rapidly to the spot where she was expected to enter the water, where he rubbed against her even more energetically as she came down. This sequence of events was often repeated a number of times before both animals reverted to swimming together quietly. Since after such activity the female immediately rejoined the male and continued to swim close to him, and because copulatory activity often followed such a display, it is possible that the display aroused more intense activity on the part of the male.

In the case of an unpaired female, however, the situation was quite different. At various times an unpaired female was seen engaging in somewhat unusual activities, such as scraping her ventral side along the bottom of the tank on the coquina gravel, and rubbing her genital area vigorously and repeatedly over the brushes, which are set up in the tank as back-scratchers for the animals. These actions have led the observers to suspect that such a female was in a state of high sexual receptivity, and in some cases this opinion has been confirmed by her subsequent actions. An unpaired female in this state often postured before the male, and sometimes initiated stroking and rubbing activities. She approached him from all angles and attempted to maintain physical contact with him. She was often very persistent in these activities even though the male paid no attention to her. She nuzzled and mouthed his genital region, and this latter behavior was sometimes followed by an erection on his part. If this happened, she often stationed herself within his line of vision and remained motionless in the water, her ventral side toward him as if inviting his attention. If he did not respond, she sometimes repeated some or all of these actions. In addition, she sometimes sought out the younger of the two males, who just reaching maturity, and initiated these activities with him. Since this younger male was often rejected as a sexual partner by the mature females, he usually responded to such attentions, and if he did so, the female allowed him to begin copulatory behavior. Such a female was seen to hang motionless and almost vertical at the surface of the water with only her blowhole exposed, while the younger male persistently engaged in copulatory behavior. Usually he was not completely successful. At times, the mature and dominant male was attracted to the scene of this activity, and participated in it himself, in which case the two males alternately approached the female.

COPULATORY BEHAVIOR

The males exhibited erections during the more vigorous phases of sexual activity. Erection and the copulatory pattern often followed the leaping display of the female or a period of strong rubbing.

The copulatory activities which have been observed may be divided as follows: erection, approach, intromission, ejaculation, and withdrawal.

Erection.—The penis of the Bottle-nosed Dolphin erects suddenly (1 to 2 seconds), the body of the organ curving outward and ventrally from the genital slit in which it is ordinarily enclosed, followed by the tip which springs rapidly away from the body. The erect penis is directed cranial, and deviates from the longitudinal axis of the animal an estimated 20 degrees to the left.

Approach.—Because of the sinistral deviation of the penis, the male usually approached the female on her right side, and partially rolling on his right side, brought the penis close to her genital opening. He approached from the rear and parallel to her, at an angle perpendicular to her path, or at any angle between these two extremes. He swam toward her, dorsal side up, rolling over as he approached her, or he turned on his back at a distance and swam toward her in that fashion. Sometimes he approached from her left side but this was unusual.

At his approach, the female did any of three things. Sometimes she swam away from the male, or continued swimming at his side, without changing her position or speed. In both of these cases, entry was almost impossible, and the male usually desisted after a short time. At other times, she rolled over on her left side and presented her ventral side to the male, at the same time slowing her speed. This position allowed the male to effect penetration more easily.

Intromission.—(Pl. I, Fig. 5) When the male was close to the female, with his ventral surface approximating hers, he brought the erect penis into contact with her ventral side in the region of the vagina. This contact was often repeated many times before intromission was achieved, since both animals were swimming slowly throughout, and other animals and water currents sometimes caused the copulating pair to move apart. If there was no outside interference, and the female matched her speed to that of the male, intromission was effected. In most of the cases seen by the present observers, the penis was inserted no more than to half its length into the vagina.

Pelvic thrusts were often observed, both before and after intromission was effected. They usually began as soon as the ventral side of the erected penis came into contact with the ventral side of the female. They continued only as long as the contact was maintained, and at times did not occur until penetration took place. A series of these thrusts usually lasted for two or three seconds, but the series was sometimes repeated a number of times. The intromission lasted for not more than ten seconds, after which withdrawal took place.

Ejaculation.—The observers do not know whether ejaculation took place during intromission, since the animals could not be captured and sperm counts made. On one occasion, after a partial intromission of short duration such as those mentioned above, the animals broke apart suddenly, and a stream of milky fluid was ejected into the water from the penis of the male. It is thought that this was semen.

Withdrawal.—After an intromission lasting from two to ten seconds, the animals broke apart suddenly. Each righted itself and swam normally. The penis at this time was still erect. Often the male made a new approach immediately, and the above activities were repeated. Sometimes the penis withdrew suddenly into the genital slit and the two animals swam off in different directions. At other times the copulatory pattern was repeated at intervals of one to seven or eight minutes for a half hour or more.

The greatest part of copulatory activity by the bull took place at night or in the early hours of the morning. It is not certain whether the reason for this lay in the diversions created during the day by feeding periods or whether it was the result of nocturnal preferences by the animals. In the past when there were fewer feeding periods the animals also tended to copulate at night. Their behavior in the wild in this respect is, of course, unknown.

Just after dawn on March 1, 1953, a member of the Marine Studios staff reported seeing a copulation between an adult male and a mature female. Although he did not observe the two coming together, he reported that the male swam on his back beneath the female. The ventral surfaces were closely pressed together so that the penis of the male was not visible. This position was retained for about thirty seconds. When the pair broke apart, the penis of the male was erect. No traces of the ejaculate were seen in the water. Since the female involved produced an infant the following spring, it is

possible that it was at this time that conception took place. This, of course, is far from certain and such data can be used only to narrow the time of conception to within a week or two, since the female was paired with the male during that period of time.

The single instance described above was of longer duration and there was complete penetration of the penis. Those seen by the present observers were of shorter duration and involved partial penetration. The observers were not able to determine whether the single instance was a typical copulation and the others incomplete, or whether a short copulation with partial penetration is typical and the single instance atypical.

There were certain complicating factors involved in such observations, since other animals were attracted to the site of copulatory activities. Young males, particularly, exhibited erections and competed for the female by crowding and pushing one another aside. In addition to interfering with the copulating animals, they also effectively obscured the view of the observers.

BEHAVIOR DURING GESTATION

Since the report of McBride & Kritzler (1951) five conceptions have taken place and the resulting pregnancies have been carried to completion, each terminating in the birth of a normal healthy infant. Four of these were recognized during the latter months of the gestation period. These resulted in the four births during the spring of 1953. The fifth (1954 birth) was recognized as a possibility from the time of conception, and its progress recorded throughout.

"Spray," a young female, was born at Marine Studios on February 26, 1947, and was the first normal infant porpoise born in captivity. She was, from the first, a healthy animal and despite bruises and lacerations inflicted on the day of her birth by sexually aroused males in the tank, she grew and progressed normally. She was a gregarious animal, and learned early to participate in all of the activities of the other animals, as well as to respond to the attentions of human beings when members of the staff played with her. Although McBride & Kritzler believed that she might initiate her first pregnancy in the spring of her fourth year, it was not until the spring of 1953 (the beginning of her seventh year) that this event took place.

On February 10, 1953, the only adult male dolphin in the tank began to show a persistent interest in Spray, and continued to seek her company for the following 13 days without eliciting any interest on her part. He was heard yelping on several occasions, also without any response

from her. He continued his pursuit of her, and on February 23 they were seen swimming together for prolonged periods for the first time. At this time the "courtship" took on what might be considered a typical pattern, including all the types of precopulatory behavior described in the previous section. Yelping by the male was often heard and Spray responded to it during this period. In addition, Spray was often seen leaping out of the water, followed by the male who persisted in keeping in close physical contact with her. No erections were seen during this activity. Early on the morning of March 1, it was reported that the bull and Spray were seen copulating. No further such incidents were reported, although it is probable that others took place. The two kept up their close association until about March 9, when it was observed that they were no longer constantly together. During the several days following this, the association was abandoned except for occasional short contacts, and for the remainder of the spring season the two animals were rarely seen together, each seeking the company of other dolphins. The male was seen either alone or in the company of other females. Spray reverted to her most consistent occupation, swimming with one or another of the new infants.

In the spring of 1949, a male infant was born to another of the adult females. From the time of his birth, Spray was almost constantly in his company, and took on the role of playfellow, not only to him, but to all of the later infants born in the tank. She often remained with them when their mothers were at the feeding platform, and was often seen swimming about the tank with them when their mothers were otherwise occupied. It was natural, therefore, that she should continue this occupation with the infants born in 1953, and she continued in these activities well into the summer.

It has been reported in McBride & Kritzler (1951) that during the latter half of pregnancy, the female tends to withdraw from association with others. In the case reported in that paper, two females, both pregnant, spent most of their time together, apart from the rest of the tank population. In the present case there were no other pregnant females present. Although Spray was often sought out as a companion by other members of the tank community, she showed an obvious preference from her earliest days for the company of her mother, "Mona," and this preference has continued to the present. Therefore, when she began to withdraw from the company of the other animals, she sought her mother as a companion. The first sign of this association, which was to continue throughout her pregnan-

cy, was seen on June 27. On that day it lasted for only a short time, but was repeated on July 1, July 3 and again on July 7. Thereafter it became a more regular companionship, and the time Spray spent with Mona gradually increased from a few minutes a day till, toward the end of her pregnancy, almost all the time she spent in company was with her mother. The remainder of the time in company was spent with "Pudgy," another mature female, and her recent infant, "Mitch" with both of whom Spray had spent much time since the infant's birth in May, 1953. Although closely observed throughout, it was seldom after July 8 that she was seen in the company of any other animal, and when such instances occurred, they lasted for brief periods only. It was also noted that in most of these instances, the other animal involved approached Spray, while she displayed little interest in seeking out other company. At this time and thereafter throughout her gestation, it was also noted that her activities decreased in vigor, and she adopted habits that were slower and more leisurely.

On June 30, the increasing roundness of her abdomen was noted for the first time, and although the animals have been known to gain and lose weight for various unknown reasons, at this time the possibility of her pregnancy became, in the minds of the observers, a probability. Pl. II, Figs. 6 & 7, show the difference in contour between a non-pregnant dolphin and one in a late stage of pregnancy.

On October 2, it was noted for the first time that Spray's mammary glands showed perceptible growth, and the area just forward and on each side of the genital opening, which had heretofore been rather flat and undemarcated from the surrounding region, now became rounder and fuller, as the glands increased in size. This definition of the glands became greater as term approached, although the glands never reached the size of those of some of the other mature, lactating females.

On December 9, straining or body flexion was observed for the first time in this pregnancy. Straining always occurred when the animal was in the horizontal position, often when she was swimming. If the animal was resting at the surface she remained there, with only the blowhole out of water. If she was swimming below the surface, she usually came to a complete halt. The flukes and caudal peduncle moved ventrally (Pl. II, Fig. 8), and as the flexion reached its maximum, the tail approached an angle of 45 degrees from the horizontal, forming an angle with the body of about 135 degrees. Often the head also bent ventrally, and as the strain

reached its climax, the entire body formed an arch, and the muscles appeared to be taut. This position was held for a few seconds. When the animal relaxed, the tail passed the horizontal and was raised dorsally, where it was held up at an angle almost as great as in the other direction (Pl. II, Fig. 9). This recurved position was also held for a few seconds, and then the animal relaxed again and swam off in normal fashion. The arch might occur without the recurve but the recurve never took place alone. Although body flexion has been seen in animals other than pregnant females, it is most noticeable in such females, and is considered a characteristic action in the latter months of pregnancy because of its repeated appearance. It was not until January 12 that Spray was seen straining again, but after this date it was seen often. From the beginning of February, flexions were seen to occur at the rate of about one a day, gradually increasing in frequency until the rate was two or three a day by the middle of the month. Toward the end of February, the total number of flexions per day increased, and the pattern changed substantially. During this period Spray might go through an entire day during which no flexions were seen by the observers, while on another day she could be observed to strain almost continuously for an hour or more, about two or three minutes elapsing between flexions. A period without flexions then followed, succeeded in turn by another period in which straining was frequent. This pattern continued until just before the birth took place, and as term approached, the periods of flexion succeeded each other with decreasing periods between until just before term, when Spray was recorded as straining almost continuously throughout several hours every day. On the morning of the day before she gave birth, she was seen to flex seventeen times in thirty-seven minutes.

As term approached, there were also other activities in which Spray was seen to participate, and which were not usually seen in non-pregnant animals. In a number of instances, she came down over the brushes which were anchored to the floor of the tank and applied her ventral side to them, scratching vigorously. At times she was seen to actually insert some of the bristles into the genital opening and wriggle back and forth over them. She also glided down to the piles of rocks on the floor, and as she approached them, she lowered the posterior end of her body, so that she bumped her ventral side against them with considerable force. Twice she did this with such force that large rocks were displaced. The activities could, perhaps, be correlated with increased vaginal irritation or tension.

During the latter months, Spray's size increased considerably, especially in the abdominal area. Although porpoises, which are exceedingly streamlined animals, do not show the distortions in body shape exhibited by some other animals during late pregnancy, even casual visitors to the exhibit were able to observe her greater girth and often commented upon it. At this time her navel, which is normally a slightly depressed scar, became slightly elevated from the body surface. Formerly a fast and graceful swimmer, she became at times almost clumsy in her body movements.

Several weeks before the birth Spray was observed to change her habits of respiration. She frequently rose to the surface, and hovering there, respired a number of times in succession, the total time elapsed being about two or three minutes. Thereafter, she resumed normal swimming. A minute or two later the behavior was repeated. This might be followed by an interval of normal breathing. As term approached the unusual breathing pattern became more frequent, and consequently she came to spend most of her time swimming at the upper level of the tank quite close to the surface. Only occasionally did she descend to the floor, usually to rub herself over the brushes or rocks. During this time she was also observed to open her mouth widely at intervals, as if yawning, and she sometimes projected her tongue beyond the tip of her upper jaw, as if licking it. She did this while beneath the surface of the water, and its significance is unknown.

At this time there was also an increase in the number of defecations per day. This number increased until during the last few days before birth defecation was almost continuous. Normally the animals defecate after feeding, and occasionally between feedings. Since the feces dissipate rapidly into the water, it was difficult to estimate the amount, but it is believed that the total amount of feces was also increased. It is probable that the increased numbers of both respirations and defecations were caused by pressure of the growing uterus upon the other internal organs. Feeding continued normally throughout this time and through the day preceding the birth.

During the last few weeks, any exertion on Spray's part produced another visible sign that parturition was not far off. During flexions, or during the spurts of vigorous swimming in which she occasionally indulged, the vaginal opening, ordinarily a closed slit, was seen to dilate to a width of about a half inch to an inch (Pl. II, Fig. 10). As term drew near, these dilations became more frequent and also more pronounced. The

opening widened to approximately two inches and the dilation sometimes lasted as long as five to ten seconds before relaxation set in.

During this last month the movements of the infant inside Spray's abdomen were easily seen. At times, distinct bulges could be seen on various parts of her abdomen, bulges which shifted from place to place, sometimes in a matter of seconds. When this happened distinct movements could be observed which were not due to the action of the mother's muscles. When a particularly violent movement of the foetus took place, she often halted abruptly and waited in mid-stroke until the movement had stopped and the foetus was quiet again. On February 4, a bulge appeared on her abdomen, posteriorly and ventrolaterally on the right side. This was persistent, lasting for several days. On February 13, Spray's contours changed again, and evidently the foetus was now situated more anteriorly than had previously been the case, since bulges were seen on both sides in the anterior part of the abdomen. Later the foetus shifted more to the left, and on February 23 an area on her left side just behind her flipper was noticeably protruding. This condition persisted until the time of parturition.

PARTURITION

On the morning of March 4, both observers were called to the tank at 5 a.m. The birth was observed to begin at 4:55 a.m. by a member of the Marine Studios night crew, who had been previously alerted as to the imminence of the event. Spray was seen swimming slowly and normally around the tank with her mother, Mona. The flukes of the infant were protruding from the vaginal opening and were lying in a horizontal plane. Most of the other animals in the tank were acting normally, and only when one of them came close enough to touch Spray or the baby did she speed up or swim evasively. At 5:15 a.m. the flukes turned at right angles to their former position, and the infant was seen to be lying on its left side. At 5:20 a.m. about three-quarters of the caudal peduncle had emerged. As she swam, Spray flexed mildly and the foetus emerged still further, but as she relaxed, it receded again. The situation continued in this way until 5:40 a.m., when the entire length (about 14 inches) of the caudal peduncle had appeared. Pl. II, Figs. 11 & 12, show two stages of birth. At this time Spray was still swimming slowly, but in a normal fashion, with Mona. At 5:43 a.m. there was suddenly a great deal of excitement in the tank. The animals gathered in the center amid whistling and a variety of other noises. Although banks of lights had been set up in the event of a birth at night, the excited racing of the

animals and the flurry of bubbles in the water which this produced, plus the darkness of the hour, kept the observers from seeing what took place during the exact instant when the infant fell free from the mother. The infant was first seen at the surface a few seconds later, against the light at the far side of the tank. The total time elapsed was 48 minutes. A minute or two later the animals had again broken up into groups, and the infant, a female, was seen swimming uncertainly, but energetically, between the dorsal fins of Spray and Mona. The baby's dorsal was inclined to the left and her flippers and flukes were soft and flabby. A number of vertical creases without pigment were seen along her sides. This is characteristic of newborn dolphins. A few minutes later, at 5:47 a.m., the adult male, possibly aroused by the birth, gave chase to Mona, and her place beside the baby was taken by Pudgy, the other female which had spent much time with Spray during her pregnancy. Shortly thereafter, however, the bull turned his attention to Pudgy, and Mona returned to swim with Spray and the infant. These three continued together, and the two adult animals guarded and guided the new infant throughout the first days of its life.

As soon as it became light, the skin of Spray's abdomen was seen to be patterned in a series of fine wrinkles, as in crêpe paper. Probably this was the result of the strong contraction of the muscles beneath, which resumed their normal tonus before the skin could do so. The crêpe paper effect lasted for several days before it disappeared.

At 9:15 am. Spray, who had been swimming slowly with the infant and Mona, suddenly speeded up and raced across the tank. This was the first rapid swimming she had done for several days, and as she did so the placenta emerged from the vaginal opening as though forcibly expelled. There was no blood visible as it was ejected, and Spray paid no further attention to it. Immediately after the placenta was expelled, Spray slowed down again, and swam off with the baby. She did not approach the placenta again.

At 10:55 a.m. the new infant began to nuzzle her mother's side. Spray neither slowed down nor rolled over at this time. At 11:18 the baby nuzzled again, this time more persistently, but without success. Again Spray did not cooperate. At 1:00 p.m., however, Spray rolled over on her side and adjusted her speed so that her mammary region was close to the baby's snout. The infant displayed no reaction to this, and did not nurse. At 1:22 p.m. the baby nuzzled again. This time Spray rolled over, and after several

thrusts of her snout, the infant found the nipples, and suckled successfully for the first time (Pl. III, Fig. 13). Another nuzzle a minute or so later was unsuccessful, but others shortly thereafter and later in the afternoon showed that the young one was locating her objective more rapidly. Within 24 hours she was seen to suckle regularly without any preliminary searching.

In 1953, the year previous to the parturition just described, four other births occurred. Each of these produced a normal, living infant. All the conceptions took place in the tank at Marine Studios. There were certain features in which each differed from the one just described.

During the last few days of January, 1952, Mona was observed to be spending most of her time with the adult bull porpoise, and was reported in copulation with him at that time. Shortly thereafter, she ate very little for a period of almost a month, although still in the company of the bull. She remained with the bull through most of February, although observations indicate that during the latter half of February it was Mona who sought the bull's company, rather than the reverse.

It was only in November, 1952, that her increased size attracted attention to her condition. On February 6, 1953, Mona's abdomen showed a shallow, concave area ventrally between the region of the navel and that of the mammary glands, which could be seen only when viewed from the side. Anterior to this region the distension of her abdomen was conspicuous. This concavity did not appear on Spray, and its significance is not known, though it may be concerned with the position of the foetus in the uterus. Some time during the night of February 6, a female infant was born to Mona, and when first seen the next morning, she was swimming between the dorsal fins of Mona and Spray. By that time the dorsal fin of the infant was already stiffened and upright, so that it could not be determined to which side it had inclined. Also, the placenta had been passed, and the baby was suckling regularly. The infant showed five deep transverse creases on the left side, six on the right. All of these were much lighter than the rest of the animal. The skin of Mona's abdomen showed the fine wrinkles which are characteristic of the new mother.

Although "Mrs. Jones," a mature female, was not observed to spend more than a day or two with the bull in the spring of 1952, abdominal distension in November of that year made it evident that she, too, was pregnant. On February 14, 1953, she was reported to be straining and dilating her vaginal opening. During this month she spent most of her time either

alone or with Pudgy. On three occasions before the birth, Mrs. Jones showed flexion and on two of these dilations were also observed. She showed no concavity in the posterior abdominal area. On February 23, she gave birth to a female infant during the afternoon. When the infant was first seen, shortly after 4 p.m., its dorsal was inclined to the right. The mother showed the characteristic wrinkling of the abdominal skin.

On February 11 and 18, 1952, the bull's courtship activities were observed to be directed toward "Susie," another female, and she responded to his yelps. In November it was noted that Susie was pregnant. On February 6, 1953, the shallow concavity was seen on her abdomen. This persisted until she gave birth. During the latter months of her pregnancy, Susie was not accompanied by another female, but swam alone and avoided the company or contact of any other animal. She flexed intermittently during the month before parturition and her genital slit dilated when she strained or when she broke into a rapid swim. She was also seen to defecate often and copiously during the last few days before birth.

Early on the morning of February 27, she gave birth to a female infant, whose dorsal fin was inclined to the right. Susie was not accompanied by any other female on the morning of the birth in spite of attempts made by Pudgy to remain near her, and she cared for the infant without the aid of any other animal. This was quite unusual, considering the conduct of all the other mothers on which data are available.

Late in April, 1952, Pudgy was seen in the company of the bull for several days. It was not until April, 1953, that her pregnant condition was suspected. Although she was the stoutest animal in the group, her weight was well distributed over her entire body, and the roundness of her abdominal region was not outstanding. Her previous pregnancy had gone unsuspected until May, 1950, when she gave birth to a male infant. Therefore, when her size increased in April, 1953, and especially when she avoided the company of other animals, she was again suspected of being pregnant, despite the absence of other symptoms.

On May 5 and 6, Pudgy was seen in the company of Spray, but with no other animal. On the 6th, she flexed a number of times. On the morning of the 7th, she strained almost continuously, and between flexions rose to the surface where she hung, respiring frequently in a pattern similar to that shown by Spray. At this time the shallow concave area was seen on her abdomen. During the afternoon of the 7th, Pudgy gave

birth to a male infant. The birth began at 2:30 p.m. when two or three inches of the baby's flukes were seen to emerge immediately after a strong flexion. At this time Mrs. Jones was swimming beside Pudgy. The following outline, extracted from the notes taken on the day of the birth, give a clear picture of the events during this parturition.

- 2:30 p.m. Pudgy arches and recurves. Suddenly there appear approximately 2-3 inches of the baby's flukes. Pudgy contracts abdominal muscles.
- 2:35 p.m. Pudgy swimming slowly in center of tank. 3-4 inches of flukes showing. Flexion.
- 2:37 p.m. Flukes completely visible. Horizontal, but tips curled ventrally.
- 2:38 p.m. Pudgy swimming close to floor of tank with Jones. She flexes and recurves. Other animals nosing around at distance of 2-3 feet.
- 2:40 p.m. Pudgy almost scrapes the bottom with her ventral side. Slows down till barely moving.
- 2:43 p.m. 2 inches of caudal peduncle showing. Pudgy maintains steady unhurried rate of speed.
- 2:45 p.m. 3 inches of caudal peduncle emerged. Jones with Pudgy.
- 2:47 p.m. Pudgy flexes. Spray swims just behind and below Pudgy, her head pointing upward.
- 2:50 p.m. 4-5 inches of caudal peduncle have emerged. All other animals quiet. Pudgy strains.
- 2:51 p.m. Foetus slips back an inch or two.
- 2:55 p.m. Foetus has turned, now lies on its right side.
- 2:57 p.m. Pudgy swimming close to surface and wall.
- 3:02 p.m. 5-6 inches of caudal peduncle have emerged.
- 3:07 p.m. Feeding show in progress. All animals rushing around.
- 3:08 p.m. Diver feeding underwater. All animals feeding except Pudgy, who swims in circles away from points of disturbance. Pudgy alone. Infant's tail hangs limp.
- 3:15 p.m. Still 5-6 inches of caudal peduncle showing.
- 3:22 p.m. 7-8 inches of caudal peduncle showing. Pudgy swims slowly, flexes.
- 3:27 p.m. Foetus slides partially out and then recedes as Pudgy flexes and relaxes. Pudgy is alone, swimming short circles in N. E. corner of the tank.

3:36 p.m. Pudgy now with Jones. Still 7-8 inches of caudal peduncle are all that can be seen of infant.

3:38 p.m. Pudgy flexes again, and recurves strongly, swimming partially on her right side. At this point, less than an inch of the baby's dorsal becomes visible, and in the next 4-5 seconds, the foetus is expelled, followed by a stream of blood.

Contrary to previous reports (McBride & Kritzler, 1951) Pudgy did not whirl as the infant was expelled, but continued swimming on and up toward the surface. The umbilical cord broke as it pulled taut. As in the case of Spray, all the dolphins gathered at the point where the birth took place, whistling and producing a clamor of other noises. Mrs. Jones pushed the baby out of the way of the other animals. Then she placed her snout beneath it and gave it one thrust toward the surface, where it took its first breath, 5 or 6 seconds after its birth. It is well known that infant dolphins are able to reach the surface without assistance immediately after birth (McBride & Kritzler, 1951), and there is no reason to suppose that this infant was an exception, especially as it was seen swimming immediately after the nudge. As a normal infant, it would undoubtedly have reached the surface for its first breath unaided, and the push given by Mrs. Jones was of secondary importance. Spray positioned herself on the other side of Mrs. Jones and the infant swam between their dorsal fins, Pudgy trailing behind. This situation continued for the next two or three minutes, when Pudgy moved into position beside the baby, and Mrs. Jones dropped out. The infant was energetic as it labored to keep pace with the adults. The baby's dorsal was inclined to the left. The total time elapsed in this birth was 68 minutes.

BEHAVIOR OF MOTHER AND INFANT

As stated by McBride & Kritzler (1951), and confirmed in later cases by the present observers, the newborn dolphin remains very close to its mother during the first month. During the first few days while its swimming is still uncertain, particularly in regard to direction, the infant will often stray slightly, but the mother invariably swims toward it and pushes it gently, guiding its direction until it is close to her side again, usually next to her dorsal fin. This position close to her dorsal fin is maintained by the infant during its first month or two, and gradually the baby then becomes accustomed to what the observers consider the typical rest position, under the mother's tail, with the top of its head lightly touching her abdomen. During the first few weeks, at least, the infant sleeps in the position next to the mother's dorsal fin.

The mother does not allow the young infant to come into close contact with other animals, and when one approaches, will swiftly sweep the young one away with her, usually placing it on the side away from the intruder.

After about two weeks the infant begins to swim about its mother and vary its position in relation to her. It may dart around her head, slip under her tail, or swim beside her at a distance of a foot or two. However, if the young one increases the distance between them to as much as ten feet, the mother will immediately swim toward it and reorient it toward her. At feeding time, the new mother will guide her infant to a position a few feet from the feeding platform, where she leaves it swimming in a small circle. She will approach the feeding platform and secure one fish, then rush back to the baby. Often she will not approach the platform again, but spend her time with the infant on the side of the tank opposite to the feeding platform, maneuvering herself and her infant away from dolphins who race for food thrown on the surface of the water. Because of this situation, special feedings are often provided for new mothers, who will accept fish thrown to them while swimming with the offspring after the regular feedings are over.

The four young ones born in 1953 prospered and grew quickly. Nursing began promptly and all the calves were able to find the nipples rapidly within 24 hours after birth. They suckled in the general pattern noted by McBride & Kritzler (1951), three to nine times within as many minutes, followed by an interval of 10 to about 25 or 30 minutes.

At about two weeks of age all the babies began to move away from their mothers, and were repeatedly retrieved. As mentioned under Spray's behavior during pregnancy, she spent a good deal of her time in the company of the young dolphins. From the time they were less than a month old, she was seen swimming with them and their mothers, and often swept away each of them with her in a rapid trip around the tank. If any other animal came close to one of the infants, the mother promptly showed her displeasure by slapping the intruder with her flukes, or by swiftly removing the calf from his vicinity. However, each mother soon allowed Spray to escort her infant without evidence of concern, and Spray usually returned the infant to its mother within a minute or two.

When Spray had been accepted as a trusted escort for the infants, all the mothers occasionally left their calves in her company while they were occupied at the feeding platform, and she was often seen surrounded by two, three or four

youngsters at this time. In addition, one mother could sometimes be seen guarding a group of infants while the others fed (Pl. III, Fig. 14). The mother who had received her food then returned and relieved the escort so that she could get her share. At the end of feeding time, each mother retrieved her own calf, and there was never the slightest hesitation about picking her own infant from the group. No mother was ever seen to make a mistake and choose the wrong infant.

By the time they were six weeks old, the young dolphins were swimming away from their mothers regularly, and associating with each other or some of the adult animals. Their mothers, by this time, had relaxed their vigilance somewhat, and the infants were no longer kept within a few feet at all times, although they were still kept under close watch. A short excursion or play period was usually followed by a longer rest period spent under or close to the mother. The infants began to show an interest in the objects and fishes in the tank and were seen to investigate, and if small enough toss about, any new object which came to their attention. If the object was a familiar one in the tank, a bit of rock, a turtle, or a small fish, the mothers watched nearby while the calf investigated, and sometimes joined it. However, if the object was an unfamiliar one, such as a new animal, or an object dropped by a visitor, the mother displayed agitation and set up a loud and continuous whistling while steering the young one away, and only when she had removed the baby from the disturbing object did she resume her normal behavior. This extreme vigilance and care were typical of the dolphin mother during the first months of her infant's life, and continued in somewhat lesser degree throughout at least the first year.

In direct contrast to the above situation, Spray showed a distinct lack of care toward her infant born in 1954. At first the situation seemed normal. The baby began to nuzzle her mother's side, as stated above, five hours after birth, and it was 2 hours and 27 minutes after this initial effort that she began to suckle. After this, nursing proceeded successfully, and the baby suckled in the same general pattern as the above infants. The baby seemed to be in good health and swam strongly from the first.

After a few days, however, it was seen that she was not growing as other infants had done. Newborn dolphins lose their thin appearance quickly, and after a few days their necks become less distinct and their abdomens become rounded. This was not true in the case of Spray's infant.

In addition, Spray did not care for the baby

as vigilantly as other mothers had done. She remained at the feeding platform throughout almost the entire feeding, returning to the calf only once or twice during this five- or six-minute period. The infant was alone during this time, except for the momentary visits of her mother.

On March 13, Spray's infant attempted for the first time to swim away from her mother. Spray and Mona swam after her, but did not hurry to her side. This, too, was in contrast to the conduct of other dolphin mothers. On March 14, the baby persistently left Spray and swam among the other animals. If she strayed more than about twenty feet away, Spray brought her back, but if she stayed within this distance, no attempt was made to restrict her movements. Twice, however, when she strayed to the other side of the tank, Spray went to her. Then Spray turned on her back, positioned the baby on her chest between her flippers, and rose to the surface, pushing the young one out of water. Other dolphin mothers have been seen to do this when their young infants swim evasively away. The effect is to temporarily immobilize the young one.

On March 16, Spray left the baby entirely alone during the feeding. On this date, the infant nuzzled its mother's side immediately after the feeding, but several minutes elapsed before Spray slowed down to allow her to suckle. On March 17, Spray allowed the infant to swim around alone for several ten-minute periods. On that day, the baby appeared to be nursing almost continuously, only very short intervals elapsing between periods of suckling.

On March 18, the baby left Spray several times, and sometimes entered another group of dolphins. Spray did not follow her, but allowed her to work her way out of the group alone.

During the morning of March 19, the infant alternately remained close to Spray and persistently suckled, or wandered far away from her, while Spray was occupied with other animals. At these times, Spray did not bring her back or swim after her. The baby was seen to suckle several times at 9:30 a.m.

At 12:15 p.m. it was reported to the observers that the infant was in distress, and both hastened to the tank. Unfortunately, by the time they arrived, a minute or two later, the infant was dead, and it was necessary to gather reports from eyewitnesses, and to attempt to fit together whatever facts could be supplied by them into a coherent account.

Early on the morning of the 19th, it was reported by an employee of Marine Studios that Spray and another unidentified dolphin, prob-

ably Mona, pushed the baby down to the floor of the tank. By moving their bodies over her, they temporarily prevented her from rising to the surface. There was no apparent reason for this action, and its significance is not clear. This report was substantiated by two other employees who happened to be looking into the tank at the time. Since both observers had seen the infant following this incident, and she appeared to be in good condition, no particular importance was attached to it at the time.

At about 12:06 p.m., the infant swam to the surface to breathe, apparently under her own power. Spray met her as she came down, and the two rose to the surface again, Spray pushing the young one up ahead of herself. As the baby sank, the second time bubbles of air streamed from her blowhole, and she did not swim again. Spray pushed her about the tank, nudging her up toward the surface every minute or so, but the infant did not breathe again. The baby's mouth opened and her tongue hung out to the side. The above account came from another employee who was watching through the port-hole at the time, and it was at this moment that the authors arrived on the scene and it was observed that the baby was dead. A diver entered the tank immediately to bring her out. Spray actively avoided the diver and pushed the dead calf ahead of her, but the body was finally taken from her and removed from the tank. From the time the infant was first seen to be in distress to the time when she was removed from the tank, only 12 minutes had elapsed. The body was taken to the laboratory and an autopsy was performed. This revealed that the calf was extremely thin, her stomach was completely empty, and she had suffered a fractured left mandible. Her lungs contained water, and it was therefore assumed that the immediate cause of death was drowning. Judging from the extremely fresh condition of the fracture, it is believed that the accident that caused it must have taken place within 24 hours of her death. At the time of her death at the age of 15 days, the infant measured 42.5 inches in total length, and weighed 30 pounds. Her weight may have been slightly less than normal for her age, since she was very thin. She possessed eight hair follicles on the left side of her snout, and six on the right side, but only one vibrissa was visible, in the last hair follicle on the right side. No structural abnormalities were found at the autopsy.

Whatever the reason may have been, Spray's infant was not receiving the usual amount of care that is given to newborn dolphins. Her mother left her for unusually long periods of time, and failed to remove her from situations in which she might have been injured inadvert-

ently by the other animals. On March 13, the baby swam directly under the platform while the other animals were feeding, and was struck by at least one dolphin falling back into the water. On March 18, while Pudgy and the bull were engaged in some of the more vigorous courtship activities, the baby swam between them, and may have been lashed by a tail before she found her way out. In neither of these instances did Spray make any attempt to rescue her young one, and it is possible that the latter incident was the cause of the infant's fractured mandible.

Two of the 1953 infants died before the end of their first year, one by accidental drowning, and the second because of an unknown infection, on which an investigation is being carried out at the present time. The remaining two young dolphins born in February, 1953, were weighed and measured in September of that year, and their lengths at that time were 68 and 69 inches, their weights 146 and 141 pounds. At the present writing they are 16 months old. They still nurse regularly, usually after feeding time, although it is thought that they are about to end the nursing period, since they occasionally skip a nursing. They began to take small pieces of squid in August, 1953, and early in December they were observed to swallow fish for the first time. Since then both young dolphins have developed excellent appetites for fish and eat them regularly at feeding times. The nursing period usually ends gradually over a period of months as the young animals show an increasing preference for fish. They race the adults for the fish even after their appetites have been satisfied. They have often been seen to rush for a fish thrown to them, then drop it to race after another on the other side of the tank. They seem to make a special effort to take fish from just in front of another animal, and often do so. They may play with the fish so taken in a number of ways. They will drop a dead fish in front of the rocks where the small tank inhabitants hide, and just as they come out to eat, the young dolphin will snatch the fish away again, only to repeat the performance a minute later. The young animals indulge in this type of sport only after they have eaten and are satisfied, but often the fish are caught by a still hungry adult and the youngsters are deprived of their plaything. Every activity of the young animals now in the tank shows them to be normal healthy dolphins.

DISCUSSION

The dolphins are a specialized group of mammals adapted in both structure and function to a life lived completely in the water. Superficially,

they resemble fish. Their forelimbs are flippers, without use as grasping organs, and probably serve mostly as balancers, or in steering. They possess no hind limbs. Their tails, furnished with broad horizontal flukes, are excellent propulsive organs. Their streamlined form enables them to move gracefully and rapidly through the water.

Since they were derived from land mammals, they bear their young alive in typical mammalian fashion, and suckle them for an extended period of time. They also display mammalian care for the young. Since they possess no limbs which can be used as manipulative organs, their mouths, which are provided with a set of efficient teeth for holding their prey, serve also to grasp objects and to inflict wounds in their own defense. The powerful muscles of the tail also aid in defense.

Together with these features, the dolphin possesses a highly developed and exceptionally large brain, of which the largest part is cerebrum. The brain of one nine-months-old *Tursiops* weighed 1230.4 grams, and its volume was 1225 cc. The length of this male specimen at the time of its death was 64 inches, and its weight was 137 pounds.

The large brain and the probable resulting high level of adaptiveness might be expected to lead, in animals with manipulative limbs, to complex varieties of behavior. The lack of these limbs results in the ingenious use of flukes and flippers. These can be delicately adjusted to produce minute changes in movement and position. Such changes enable the animal to make the best possible use of the only grasping organ it possesses, the mouth. The remarkable use of these organs under the control of a well-developed central nervous system leads to behavior patterns which are peculiar to these animals and their close relatives.

No accurate observations on the precopulatory and copulatory behavior of dolphins were possible before the tanks at Marine Studios were established, and therefore such observations as were available were recorded by whalers and transmitted to interested scientists, or such scientists reported their own observations from the decks of ships. Lillie (1910) reported that whalers saw two adult sperm whales (*Physeter*) rush together near the surface, then turn up vertically at the end of the rush. They believed that they had seen copulation, and said that the males were exhausted and easy to capture after these activities. Morch (1911) observed coition in blue whales during the summer, but gave no details of their behavior. Tomilin (1935) noted what he considered to be sexual attachment in various species, and differences between the species and

between individuals in the same species. He stated that this attachment sometimes reached great intensity and was strongly shown especially if one of a pair was wounded. He gave no details of copulation. Hamilton (1945) reported that while sailing off the coast of Brazil, he saw two *Steno* swimming on their sides with their genital areas pressed together. They were slightly separated anteriorly, and one's mouth was slightly open. This posture was maintained while they remained in sight, which, according to the author, was "not for very long." The ship was moving at 10 knots, and the animals maintained the speed of the ship while in the above position.

Such fragmentary observations do not give any indication of the complex pattern of precopulatory and copulatory behavior in this group of animals and it was not until they could be observed under water for extended periods of time that details could be reported. Although many of the events leading to copulation are reported here, the sequence is variable, and it is by no means certain that copulation can be predicted following any particular stage. The observers have seen much copulatory behavior, some of it at least partially successful. In at least one instance an ejaculation of semen has been seen after withdrawal of the penis from the vagina of the female. Sudden erection and retraction of the penis occur most often during the spring months both with and without true copulatory activity, so that retraction is no indication that ejaculation has taken place during a partial intromission. The one instance in which full penetration took place occurred before seven in the morning and was not seen by the authors. The employee who witnessed it is a reliable observer who has made a hobby of watching the animals over a long period of time. It is not known whether the copulations involving partial penetration over a short time are as effective as those with full penetration extending over 30 seconds. Although the authors have spent a number of hours watching during the evening hours and also in the early morning, they have not seen the longer copulations. Since there is no provision for adequate lighting at night, observations during this time are impossible. Perhaps long-continued early morning observations over a long period of time will provide more data.

Although McBride, in 1940, recognized the jaw clapping of the bull as "the principal form of intimidation," the entire use of this sound was not recognized until much later. As late as 1948, McBride & Hebb again stated that this sound was used by a dominant animal toward subordinates. The observations of the present authors indicate that this is not always the case,

and the jaw clap has, under direct observation, been made or attempted by almost every animal in the tank. It has occurred under a number of circumstances but these were always such that the jaw clapping animal appeared to be displeased, dissatisfied or annoyed. Pudgy clapped her jaws when the bull, who is dominant to her, made sexual advances to her and she was not responsive. All the mothers clapped their jaws when another animal interfered with or approached their young. Spray has been seen to clap her jaws when the young male swam between her and the infants in her company. The younger animals, such as Spray and the young male, produce a much less resounding clap than Pudgy and the bull, but their efforts were unmistakable, and as they gained more experience and practice, the sound produced became louder. Apparently this evidence of displeasure is limited to the adults, since the 1953 youngsters have not as yet attempted it.

Townsend (1914) gives some evidence to show that *Tursiops* breeds yearly in the wild. Of 51 specimens taken in November, 34 were females. All the females taken were in milk at that time. Although he does not state how many of the females were killed, all those that were killed were not only in milk but contained young. Unfortunately, the age of the suckling infants could not be determined. Therefore, it is not known whether all infants in the wild suckle for 18 to 21 months or more, or whether there is a yearly reproductive cycle. Since young dolphins at Marineland have been known to suckle for periods up to 20 months, it is possible that Townsend's data would support the idea of a two-year cycle in the wild.

At Marine Studios, no female has as yet produced young two years in succession. Several animals have produced young at two-year intervals. There is in the tank only one fully adult male, and therefore no significant competition for females. There is the possibility that females unaccompanied by newborn young are preferred partners. It is to be hoped that some future study may show whether the two-year cycle seen at Marine Studios is unchanged from the wild condition.

McBride & Kritzler (1951) believed that the female Bottle-nosed Dolphin becomes sexually mature at four years of age and may bear her first infant in the spring of her fifth year. Although this may be theoretically true, the only evidence now at hand indicates that the first infant may not be conceived until several years later. Spray, the only animal that was born and reached sexual maturity in captivity, did not conceive until she was six years of age, and

delivered her first infant just after her seventh birthday, although she was known to be in excellent condition throughout her life. It is, of course, not known whether she would have conceived earlier in the wild, and further evidence on the age at which sexual maturity is reached will depend on the time at which the young females now in the tanks first conceive.

There has been much speculation on the length of the gestation period in these animals, and estimates which have run from 10 to 14 months have in the last few years narrowed to 11 to 13 months. It is now possible to state with a reasonable degree of accuracy that the gestation period is very close to 12 months. Spray's association with the bull lasted for a period of two weeks, from February 23 to March 9, 1953, and her infant was born on March 4, 1954. Similarly, the associations of Mona and Susie with the bull were almost exactly a year before the birth of their young ones. Although Pudgy was observed to be in the company of the bull in late April, 1952, and her infant was born in early May of the following year, the authors believe that this discrepancy comes within the limit of error, and that the twelve-month period is the most valid one.

McBride & Kritzler (1951) noted the withdrawal from association with other animals shown by pregnant females, especially during the latter part of pregnancy. They also mentioned the tendency of two pregnant females to associate with each other. These tendencies have been confirmed in the present paper. In 1952, Pudgy and Mrs. Jones, although they conceived several months apart, spent most of their time together during their pregnancies, though they had not been close companions before this time. When Pudgy's infant was born, Mrs. Jones was the animal which escorted the infant during the first few minutes of its life, and she and Spray kept the infant out of the way of other excited animals, and accompanied Pudgy and the new baby for the first few weeks. When Spray's infant was born it was Mona, her mother, and Pudgy who performed these functions alternately, so that there was almost always another mature female swimming beside the baby. Such protection proved to be important, since the records show that the birth of a young one seems to stimulate the adult male to begin or renew his courting activities. Often these are directed toward the new mother, whose evasive movements become frantic in her efforts to protect her newborn infant. In 1947, when Spray was born, there were several adult males in the tank, and in their attacks on the new mother and other females and each other, Spray's skin was badly lacer-

ated by their teeth. Since then, these competing animals have been removed, but the danger to the new infants still exists, though to a lesser degree.

In one case, however, the new mother was not accompanied by another female. Susie is an extremely retiring animal, and remained alone from the time she was first captured and placed in the tank. She conceived in February, 1952, and remained alone throughout her pregnancy, a situation which was unusual enough to warrant the attention of the observers. When her infant was born in February, 1953, she was not accompanied by any other animal. Immediately after the birth Pudgy made persistent efforts to swim with her and remain near her, but Susie avoided Pudgy as diligently as she did all the other animals. Her behavior, though unusual, was consistent, since both before and after her pregnancy she showed no inclination to associate with any other dolphin. She was captured in 1949 and gave birth three days later to a male infant, an event which took place in the receiving tank. This tank contains very shallow water, and the environment was quite unnatural to her. Her timidity may have stemmed from that time. The young male has now almost reached maturity, and the two ceased their association prior to the arrival of the new infant. It took more than a year of training before Susie took her food at the feeding platform. Either her inherent timidity or the shock of her arrival and the subsequent birth may account for her unusual conduct.

The young of members of the Delphinidae are usually born tail first. In every birth at Marine Studios except one (Spring, 1955) the infant emerged in this manner.

In the earliest papers describing the birth of small cetaceans, (James, 1914), the author assumed that the normal presentation was head first, and that it was mishandling or other improper treatment which caused the tail presentation. The birth described by James took place in *Phocaena phocaena* and was a stillbirth. James mentioned mishandling as the reason for the tail presentation, and the tail presentation as the reason for the stillbirth. It is now known that although mishandling may lead to stillbirth, the reasons are other than those described above.

Caudal presentation has been described in detail by a number of authors (Wislocki & Enders, 1941; Slijper, 1949). McBride & Kritzler (1951) discussed it in connection with data available to them from Marine Studios, and all agree that the foetus is, or becomes, oriented in such a way that the head is pointed toward the tubal end of the uterine cornu, while the tail extends toward

the vaginal opening. Sleptzov (1940) observed 635 embryos of *Delphinus delphis* in situ during various stages of development, and came to the conclusion that during early embryology the foetus may lie in either direction. Later the head tends to become oriented toward the tubal end of the cornu, and by the time reversal is no longer possible, because of size, the vast majority of embryos are situated in this way, so that tail presentation is inevitable.

The problem remains, however as to why the orientation takes place in this manner. Slijper (1949), citing Williams & DeSnoo, discusses the dangers attendant upon breech presentation in mammals which produce foetuses with comparatively large heads, and believes that the compression of the umbilical cord between the pelvis of the mother and the head of the infant which occurs in breech presentation may cause asphyxia if the infant is not quickly extracted. Although Odontocetes possess no pelvic girdle other than two small pelvic bones, the pelvic region contains large masses of tough fibrous connective tissue which could exert considerable pressure, and it is possible that such compression may be exerted in the case of these animals. Whether or not this is true, it does not explain the orientation of the foetus in the uterus, but only illustrates an effect of such orientation.

Slijper's discussion of the role of uterine contractions in the orientation of the foetus is more pertinent to the question. Mammals other than primates show, during pregnancy, uterine contractions of a peristaltic nature which begin at the tubal end of the uterus, and Slijper believes that the head should be impelled in the direction of the cervix under the influence of these contractions, in mammals with a small head and long neck. Since this formation does not apply to cetaceans, he considers that the body form of the foetal cetacean might favor caudal presentation.

Schumann (1914) discusses the possible causes of almost universal cephalic presentation. He states that in multiparous animals the foetuses lie indifferently, in either breech or cephalic presentation, whereas in unipara, the head presents in 90 to 98 percent of the cases. In man the foetal head is heaviest and gravitates to the most dependent position, nearest the cervix. In uniparous quadrupeds, however, the hindquarters and trunk of the foetus are its heaviest parts, and consequently sink to the lowest portion of the uterus, which with its cornua lies low in the abdominal cavity. The cervix rises to meet the vagina.

In dolphins, which are uniparous, the uterus lies in a situation similar to that seen in the quadrupeds, so that the heaviest portion of the

foetus would tend to gravitate to the lowest portion, the tubal end of the cornu. These animals, however, possess no hind limbs, only remnants of the pelvic girdle, and the tail is long and slender. The head, which is relatively very large, and the pectoral region are heavier than the hindquarters. Under these circumstances, the gravitation of the heaviest portion toward the tubal end of the uterus would result in tail presentation. The present authors believe that this situation may be of considerable influence in the determination of tail presentation in the dolphins.⁴

It is necessary, however, to consider the folding of the uterine cornu in evaluating this explanation. The non-pregnant dolphin uterus is not folded. Presumably the fold occurs when the foetus is too long to extend to its full length in the abdomen of the mother. At this time it would also be too large to turn easily on its own axis. Examination of the pregnant uterus of many delphinids has shown that the foetus appears, at first glance, to have its head oriented toward the vaginal end of the uterus. Closer observation, however, has usually shown that the head is enclosed in a fold, which is oriented toward the caudal end of the mother, but that on following this fold in the direction in which the head is pointing, it is found that the uterus continues from this point toward the Fallopian tubes. Following the body of the foetus in the opposite direction reveals that it folds close to the origin of the tail, and the tail occupies the lower end of the uterus, and extends toward the vaginal opening.

These facts may seem to contradict the weight theory outlined above, but if we consider that the head of the foetus, as in most mammals, develops more rapidly than the other parts, and becomes the heaviest part of the foetus in an early stage of development, before the fold occurs, it seems possible that both events might occur in sequence, with the usual observed result of tail presentation. It is unfortunate that Sleptzov (1940), who had at his disposal more than six hundred foetuses in all stages of development, did not record more fully the sizes, weights and developmental characteristics of these animals, together with the condition and configuration of the uteri in which they were found.

Although McBride & Kritzler (1951) stated that in all cases observed by them the dorsal fin of the newborn dolphin was folded to the right,

⁴Recently E. J. Slijper (1956. Some remarks on gestation and birth in cetacea and other aquatic mammals. Hvalrädets Skrifter. Scientific Results of Marine Biological Research, No. 41, pp. 1-62) reported additional data and conclusions concerning tail presentation in cetacea which confirm those given above.

at least two cases were seen by the present observers in which the dorsal was folded to the left. In one of these cases the infant was seen to be lying on its left side when only partly extruded from the mother's body. We do not know whether this correlation holds true in all cases.

The symmetrically placed vertical creases on each side of the trunk at birth are not necessarily six in number, as stated by McBride & Kritzler. In the group of births recorded here, the creases have numbered five, six or seven, and there were sometimes more on one side than on the other. Also, one or more may be continuous over the dorsal part of the animal. They lacked pigment and were easily visible for several weeks after birth, when they gradually acquired pigment and disappeared. The young dolphin to which Spray gave birth, and which died at 15 days of age, showed two creases which were not continuous over the dorsal side but which appeared on both sides, three which were continuous over the dorsal, and two ventral creases, which were not seen previous to her death because of the lack of pigment on the ventral side of the body.

It may be significant to note that the dorsal fin of the infant which died at 15 days was slightly inclined to the right when the body was removed from the tank. At birth it was distinctly folded to the left. It has been noted by many observers that the dorsal fins of all the adults incline to the right, and it is thought that the swimming tendencies of the animals may be the cause of this phenomenon. Since the animals in the tank usually swim in a clockwise direction through a counterclockwise current, the force of the water against their dorsal fins may be the cause. It should be noted, however, that this inclination in no way hampers their swimming in any other direction. It seems significant that the tilt to the right should have taken place so quickly in an infant whose dorsal was inclined sharply in the opposite direction only 15 days before.

The mother of a newborn dolphin has never been seen to eat the placenta, which is expelled several hours after birth. Since eating this organ appears to play a significant role in the behavior of so many other mammals, this point seemed to be of particular interest. In all the cases on record at Marine Studios no mother dolphin has even approached the placenta after expelling it, and unless removed by divers and preserved, the organ is torn to shreds by the turtles and fish in the tank.

Although McBride & Kritzler (1951) reported that a mother dolphin, immediately after the infant's body falls free, will whirl about and

thus snap the umbilical cord, this does not appear to be necessary in every case. At least one female in the present group spurted forward in a straight fast swim as the baby was released and the cord snapped quickly as it pulled taut. The survival value of the whirl, in case the infant fails to reach the surface, is obvious, but the pattern does not seem to be an invariable one.

The problem of suckling in the dolphin has long been of interest to observers, and the mechanism has been fairly well worked out. Milk is poured from the mammary glands into large sinusoids, which in turn open to the nipples, situated on each side of the genital slit. When the infant grasps the nipple, abdominal contractions of the mother pour the secretions into the baby's mouth. The question remained as to whether the stimulation of the nipple by the infant was necessary in order to produce a flow of milk, or whether the contraction of the abdominal muscles was under the voluntary control of the mother. An instance that took place in the spring of 1954 shows that, at least in extraordinary circumstances, the flow of milk is entirely under the mother's control. On February 22, 1954, a nine-months-old young dolphin, born the previous May, died at Marine Studios of an unknown skin infection. At the time of his death, he was still getting the main part of his food from his mother, and was only beginning to show an interest in other food. On the day before his death, he suckled very few times, and his mother's nipples protruded from their slits, apparently pushed outward by the engorged sinusoids. On the day of his death and for several days afterwards this condition continued. Twice in the first several days after the young one's death, the mother was seen to turn on her side in the water and visibly contract her abdominal muscles, raising her tail as she did so. As she did this, a stream of milk spurted from her nipples. This stream was ejected with a force strong enough to send it a distance of more than two feet before it dissipated into the water. It is not known whether such a feat can be accomplished in circumstances where the sinusoids are not filled to excess, but it shows that a female dolphin can eject milk without stimulation of the nipple under certain conditions.

Several Russian authors, particularly Khvatov (1938) and Sleptzov (1940) have reported on births of Delphinidae (mainly *Delphinus delphis*) which they observed in the Black Sea. In most of these births, the animals concerned were captured dolphins, and were seen while in seines being drawn toward shore. The rest were in shallow areas near shore. It is possible

that the births may have been abnormal in some cases, particularly in the case of the captured animals, which could have been shocked and frightened by the procedure of capture. Also the conditions for observing the births were unfavorable, since many animals were milling about in the seine, and in all cases the births were observed from above the surface of the water. In spite of these difficulties, there are descriptions of reverse flexions, leaps, dives, and in some instances, the moment of birth when the infant fell free. In all cases the infant was born tail first, but no description of the moments immediately following birth is recorded. In the most complete description, the birth took one hour and fifteen minutes from the time the author (Sleptzov, 1940) first saw the tail of the infant protruding from the mother, and the infant's dorsal fin was folded to the right. The general description of the birth is similar to those seen at Marine Studios. Khvatov, after seeing an apparently abnormal birth, observed an infant attached to its mother by the umbilical cord, and postulated that this was a normal condition. He thought that the infant suckled while still attached to the mother. In the specimens examined at Marine Studios, no umbilical cord was found to be long enough to permit such a procedure. Whether the umbilical cord of the species he studied was sufficient in length is not known, but Sleptzov, after seeing what he believed to be the same species, thought Khvatov's theory erroneous. He observed a larger number of births than did Khvatov, and in each instance the infant separated from the mother promptly with no apparent ill effects to either. All evidence from births in the wild indicates that they parallel closely those seen at Marine Studios.

The reaction of Spray toward her first infant presents an interesting problem. She was seven years of age when she gave birth to this calf. It has been thought that dolphins mature sexually at an earlier age, and therefore it is doubtful that she was too young to care for it. She had been active for several years in escorting and protecting other young dolphins in the tank and it seems reasonable to assume that therefore she had sufficient general background experience. However, never before had she had the constant care of an infant, and she had not suckled an infant before. Although the immediate cause of the infant's death was drowning, it is not certain whether the baby drowned because of a shock reaction to the fractured mandible, whether it starved until it was too weak to swim, or whether there was another reason, undiscernible to the investigators. The observers could find no abnormalities in the digestive tract to account for its thinness or its inability to suckle. Young

dolphins use their tongues, rather than their lower jaws, in suckling. The youngster was quite obviously hungry, judging from the number of times it approached its mother's mammarys, and its persistent nuzzling there. It was impossible to determine whether Spray produced sufficient milk as she could not be removed from the tank for examination. Her mammary glands remained distended for several days and gradually receded over a period of several weeks. It is possible that more evidence may be found when Spray gives birth to a second infant and her reactions to it can be observed.

Although this report contains many data that have not been previously presented, it is extremely difficult to quantify, since records of the earlier births, both by McBride and his co-workers and by the present investigators, did not contain all the details which are now considered essential to an analysis of the behavior of these animals. In addition it is probable that further details, up to now unrecorded, will later present themselves. Further observation by experienced investigators and the recording of seemingly non-essential details will produce a more complete picture, and one that will allow a more accurate comparison with other mammals.

SUMMARY

The group of captive Bottle-nosed Dolphins (*Tursiops truncatus*) at Marine Studios is an actively reproducing colony. Mating and parturition take place from February to May, usually in a two-year cycle. The report comprises the data on five pregnancies and births, one of which was observed from conception.

Precopulatory behavior consisted of a prolonged companionship between a male and female. There followed such activities as posturing, stroking, rubbing, nuzzling, mouthing, jaw clapping and yelping on the part of the male. These occurred in any sequence and if the female responded, copulatory behavior followed. This included erection, approach, intromission, ejaculation and withdrawal. Most of the copulatory activity took place at night or in the early morning, although some of the activities were seen at all hours during the day.

The gestation period was about twelve months. After about four or five months, the pregnant female tended to withdraw from the society of other dolphins, and usually established at this time the one or two associations which she maintained throughout the remainder of her pregnancy. The rest of her time was spent alone. Her activities gradually diminished in vigor, and as term approached she became slow and sometimes clumsy. Toward the end of preg-

nancy a labored respiratory pattern was seen, yawning and body flexion appeared, and defecation increased in frequency.

The infants were born tail first. The mother either whirled or swam rapidly ahead, and the umbilical cord broke as it pulled taut. The unpigmented creases on each side of the body of the infant were not symmetrical in every case, and sometimes there were more on one side than on the other. The infants swam from birth. The dorsal fin was folded sharply either to the right or left, but stiffened in an upright position within a few hours. The placenta was expelled several hours after birth. The mother did not eat it, nor did she approach it again.

Dolphin mothers kept close to their infants at all times for the first months, and removed them promptly from dangerous situations. During the first weeks, the infants were not allowed to stray more than ten feet from the mother. Nursing was established during the first 24 hours. The infants were weaned at approximately 18 months.

One female dolphin, born and raised at Marine Studios, did not care for her infant as carefully as the other mothers. She left the baby alone at feeding time and for other short periods. She did not remove it from contact with other animals or from dangerous situations. The infant died at 15 days of age.

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EXPLANATION OF THE PLATES*

PLATE I

- FIG. 1. Young male dolphin (Algie) above, and adult female (Mona) below. The male strokes the back of the female with his flippers.
- FIG. 2. Young male and female during rubbing activity. The two have approached each other head-on and their bodies will rub together (Algie and Spray).
- FIG. 3. Young male and female during rubbing activity (Algie and Spray).
- FIG. 4. Male and female during mouthing.
- FIG. 5. Adult male (Happy) and young female (Spray) in copulation. Note partial insertion of penis into vaginal opening.

PLATE II

- FIG. 6. Adult female (Susie) in non-pregnant state.
- FIG. 7. Adult female (Susie) in late pregnancy.

- FIG. 8. Adult female (Mrs. Jones) in late pregnancy, in body flexion.
- FIG. 9. Adult female (Mona) in late pregnancy. Recurve of body flexion.
- FIG. 10. Female in late pregnancy. Recurve of body flexion while rubbing over rocks. Note vaginal distension and protruding nipples.
- FIG. 11. Birth in progress. Flukes and part of caudal peduncle are seen projecting from vagina of mother.
- FIG. 12. Birth in progress. Taken just before complete emergence. Note umbilical cord, also presence of companion female on the left.

PLATE III

- FIG. 13. Suckling. Young female (Spray) and infant (Peggy) a few days after birth.
- FIG. 14. A new mother (Pudgy) escorts her own infant and two others during feeding period while mothers of the other two feed.

*Photographs by F. S. Essapian.



FIG. 1



FIG. 2

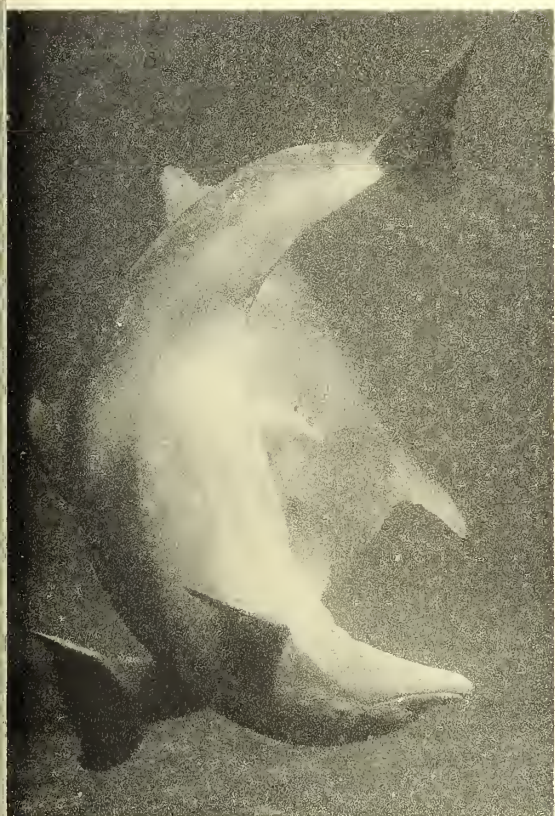


FIG. 3



FIG. 4



FIG. 5

THE BEHAVIOR OF THE BOTTLE-NOSED DOLPHIN (*TURSIOPS TRUNCATUS*); MATING, PREGNANCY, PARTURITION AND MOTHER-INFANT BEHAVIOR



FIG. 6



FIG. 7



FIG. 8

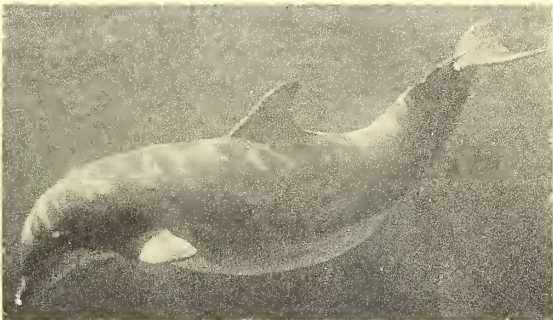


FIG. 9



FIG. 10



FIG. 11

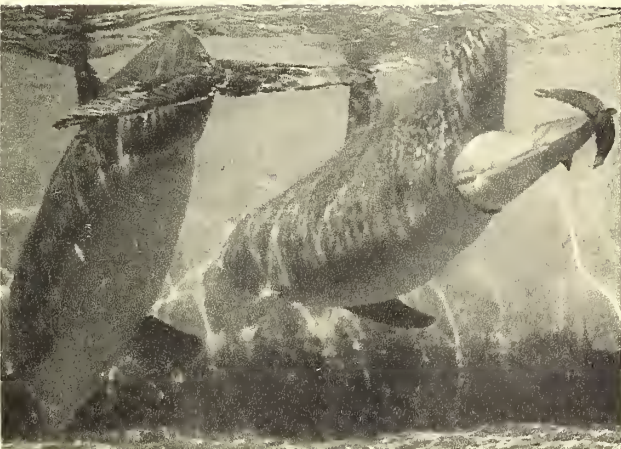


FIG. 12

THE BEHAVIOR OF THE BOTTLE-NOSED DOLPHIN (*TURSIOPS TRUNCATUS*); MATING, PREGNANCY, PARTURITION AND MOTHER-INFANT BEHAVIOR



FIG. 13



FIG. 14

THE BEHAVIOR OF THE BOTTLE-NOSED DOLPHIN (*TURSIOPS TRUNCATUS*); MATING, PREGNANCY, PARTURITION AND MOTHER-INFANT BEHAVIOR

3

A Study of the Relationship Between Certain Internal and External Morphological Changes Occurring During Induced and Natural Metamorphosis in *Rana pipiens* and *Rana catesbeiana*

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(Text-figures 1-12)

THE dramatic metamorphosis of the tailless Amphibia is the subject of an extensive literature resulting in large part from Gudernatsch's (1912, 1914) acceleration of the process by thyroid feeding, and from the subsequent discovery of the thyroid-pituitary relationship by Adler (1914), Allen (1916) and Smith (1916a). A chronology of the external metamorphic events was established by Etkin (1932), who also showed (1935) that thyroxine treatment did not change the order of events but did change their spacing. Knowledge of internal metamorphosis both normal and accelerated is quite complete, with many excellent and detailed studies of one, two, or more internal organs. However, there is no single analysis of internal changes comparable to Etkin's for the external pattern. Disharmonies in development during accelerated metamorphosis have frequently been noted, and several theories of the control of the sequence and spacing of metamorphic events have been reported (see the review of Lynn & Wachowski, 1951).

During normal metamorphosis, the rate and extent of change in the several organs are so correlated that a given degree of change in an external organ, such as the developing hind limb, is a measure of the change to be expected internally (Allen, 1929). Although the available evidence indicates that this is not true during accelerated metamorphosis, more information as to the degree of deviation from the normal correlation between internal and external changes in accelerated metamorphosis seemed desirable.

Therefore, a comparison of the development of several internal organs in normal and thyroxine-treated animals at similar external metamorphic stages was undertaken. *Rana pipiens* and *Rana catesbeiana* were both studied in order to obtain differing lengths of larval period for the purpose of comparison.

Grateful acknowledgement is made to Drs. E. G. Reinhard and W. Gardner Lynn of The Catholic University of America; to the former for interest in the problem and generosity in extending facilities for research, and to the latter for valued discussion and advice.

MATERIALS AND METHODS

1. Plan of the Study

Rana pipiens and *Rana catesbeiana* were the species chosen for study because of the difference in the lengths of their larval periods.

To compare the integration of internal and external changes in normal metamorphosis with that in accelerated metamorphosis, larval stages were selected at which the external morphology of the normal and treated animals was considered comparable. Normal and accelerated animals were killed at each of these stages and certain of their internal organs compared. Because of the occasional rather substantial variation in age between normal and accelerated tadpoles at apparently the same external metamorphic stage, untreated tadpoles of the same age as the accelerated were also killed and studied concurrently.

To select accelerated stages most comparable morphologically to normal stages, the effects of the various thyroxine concentrations were observed. It was concluded that only the forelimb emergence stage was recognizably similar to the

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normal in all series, and therefore a more comprehensive study was made of this stage. Earlier accelerated stages in certain respects overlapped several normal stages. Although accelerated animals were studied at a stage later than forelimb emergence, this later stage has been named "terminal stage" rather than "tail stub" stage as in the normal series.

The following stages were studied:

- (1). Initial stage (normal animals, 12 and 21 days old)
- (2). Two mm. hindlimb stage (*R. pipiens* only)
- (3). Forelimb emergence stage (both forelimbs emerged)
- (4). Tail stub (terminal stage)

The effects of rate of acceleration on metamorphic integration were studied by the use of two aqueous thyroxine concentrations: 1:10,000,000 and 1:100,000,000. Each has been used previously (e.g., Allen, 1932; Etkin, 1935). In addition, two age groups of tadpoles were treated with each concentration. One group was 12 days old at the beginning of treatment; the other 21 days old. Treatment by immersion was continuous.

The following groups for each stage in both species were studied and compared:

- (1). Animals metamorphosing normally in the laboratory;
- (2). Animals accelerated by 1:10,000,000 thyroxine from 12 days of age;
- (3). Untreated animals of the same age as were those in (2) when killed for examination;
- (4). Animals accelerated by 1:10,000,000 thyroxine from 21 days of age;
- (5). Untreated animals of the same age as were those in (4) when killed for examination;
- (6). Animals accelerated by 1:100,000,000 thyroxine from 12 days of age;
- (7). Untreated animals of the same age as were those taken in (6) when killed for examination;
- (8). Animals treated with 1:100,000,000 thyroxine from 21 days of age;
- (9). Untreated animals of the same age as were those in (8) when killed for examination.

At the selected stages, internal metamorphosis was studied morphologically following dissection, and the forelimb stage of *R. pipiens* by microscopic examination of serial section. The internal organs studied were:

- (1). *Tongue*: length, development, presence or absence or premetamorphic papillae;
- (2). *Intestine*: length, histology (in *R. pipiens*) at the forelimb stage;
- (3). *Gall bladder*: color, size;
- (4). *Urinary bladder*: presence, degree of development;
- (5). *Pancreas*: size, histology (in *R. pipiens*, forelimb stage);
- (6). *Pituitary*: (in *R. pipiens*, forelimb stage) size, development;
- (7). *Thyroid*: (in *R. pipiens*, forelimb stage) follicle number, mitotic activity, position.

In addition, body length, tail length and hindlimb length were recorded throughout the course of normal and accelerated metamorphosis in both species.

Because of *R. catesbeiana*'s long tadpole period, 17 late tadpoles were collected from the Kenilworth Lily Ponds, Washington, D. C., March 24, and brought to the laboratory to serve as the normal series for the stages of forelimb emergence and tail resorption. The rest of the *R. catesbeiana* tadpoles used for the study of younger normal stages and for the experimental series were laboratory raised from an egg film collected at the same place, July 2.

2. Method of Rearing and Feeding the Tadpoles

The tadpoles were reared in flat, white enameled pans (10" × 15" × 1½"). For *R. pipiens*, 20 animals were placed in each pan with 1,000 cc. of water or thyroxine solution. For *R. catesbeiana*, 10 animals were placed in each pan with 2,000 cc. of water or thyroxine solution. The thyroxine solutions and water were changed daily. Food (chopped spinach and Pablum) was provided in excess. The experiments terminated after forelimb emergence when the animals' tails were resorbed to dark stubs or when deaths had reduced the number of animals in each series to 10 for *R. pipiens* and to 5 for *R. catesbeiana*.

3. The Normal and Experimental Series

The experimental animals in each species were divided into four series. In the table below are listed the designation, the treatment and the number of animals in each series.

Naturally metamorphosing animals constituted the series designated as "SC" (Stage Controls). Separate series of untreated tadpoles were raised and observed, and individuals from these series were fixed concurrently with those from the experimental series. These constituted the "Age Controls." For *R. pipiens* there was a total of 100 tadpoles in the Age and Stage Con-

trol series; for *R. catesbeiana*, a total of 96 tadpoles.

DESIGNATION	TREATMENT	NUMBER OF ANIMALS	
		<i>R. pipiens</i>	<i>R. catesbeiana</i>
A-1	1:10,000,000 thyroxine from age 12 days	60	30
A-2	1:10,000,000 thyroxine from age 21 days	60	30
B-1	1:100,000,000 thyroxine from age 12 days	60	30
B-2	1:100,000,000 thyroxine from age 21 days	60	30

4. External Measurements

Measurements were made as often as changes in rate of development seemed to require. In both species, measurements were made daily during the course of the experiments using 1:10,000,000 thyroxine. For the 1:100,000,000 thyroxine series, generally daily measurements were made for *R. pipiens* and less frequently for *R. catesbeiana* (once a week or ten days). At such times, 10 animals in each series were measured. To facilitate the process of measuring, the normal and experimental animals of both species were anesthetized with MS 222.

5. Dissection

Two specimens of *R. pipiens* and three specimens of *R. catesbeiana* for each normal stage and each experimental stage, along with an equal number of age controls, were dissected. Gall bladder color changes and presence or absence of the urinary bladder were investigated in additional dissections made so that these observations were based on at least five dissections for each stage and series in both species. Dissection was done using 7× and 17× magnifications. The entire digestive tract was removed from the body cavity by freeing the cloaca from the ureters, cutting the mesentery and lifting the entire mass from the dorsal body wall anteriorly at the glottal level of the pharynx. Then the color of the gall bladder and its size relative to the liver were recorded. The shape of the ventral pancreas was sketched and its dimensions taken with dividers recorded on the sketch. The liver and pancreas were removed, the bile duct severed and the intestinal mesentery cut so that the entire intestine could be uncoiled. Measurement was accomplished by cutting the intestine into convenient lengths and straightening these lengths on a millimeter rule. Finally the presence or absence of the urinary bladder and its relative degree of development were recorded.

The shape of the tongue was sketched and (for *R. catesbeiana*) the anterior-posterior dimension as taken with dividers was recorded. The number and disposition of the premetamorphic papillae were also recorded.

6. Histological Study

Two animals in the forelimb emergence stage in each of the *R. pipiens* series were serially sectioned and prepared for histological study. Age controls were also serially sectioned. Specimens were fixed in Bouin's solution, sectioned in paraffin at 10 micra and stained with Masson's stain.

OBSERVATIONS

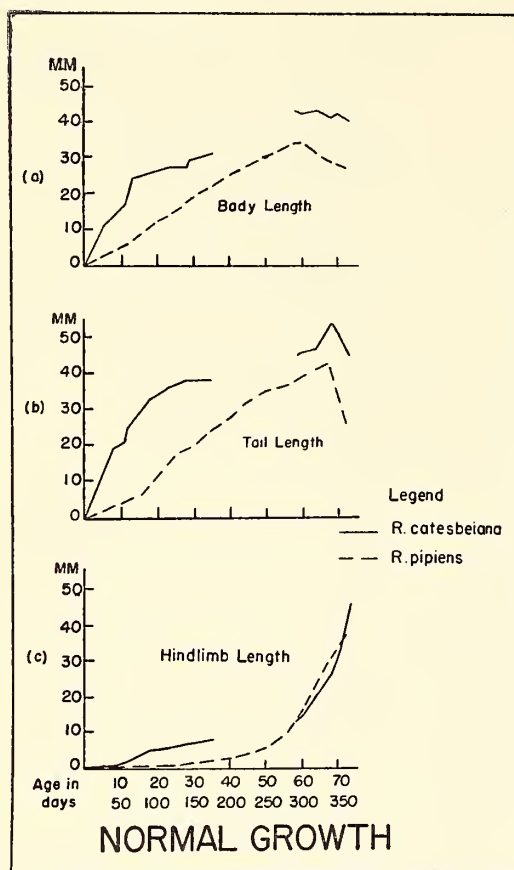
1. Growth Measurements

It has been noted already that the normal series of *R. catesbeiana* represents animals obtained at different times; (first) mature tadpoles collected in the field and raised in the laboratory through the rest of the tadpole period; and (second) tadpoles hatched in the laboratory from an egg film collected later in the season. The tadpoles from the egg film provided both the experimental series and their normal Age Controls. The Age Controls were observed during a period of 173 days and were fixed at the end of that time with the remaining experimentals. By this time, a number of the Age Controls were as large and as well developed as the late tadpoles (used as the Stage Controls) had been when collected. Therefore the growth data for the two normal groups were plotted as a single curve (Text-fig. 1) broken by a time lapse equal to that between December (when the Age Controls were fixed) and March (when the Stage Controls were collected).

The growth curves and the time required for response (Text-fig. 2) were approximately the same in both species of organisms treated with 1:10,000,000 thyroxine. The experiments terminated in death after 16 days for *R. pipiens* and 10 or 11 days for *R. catesbeiana*. With 1:100,000,000 thyroxine, the growth curves for the two species are very similar (Text-figs. 3 & 4). The number of days required for response in *R. catesbeiana* was greater than for *R. pipiens*, but, considering the normal length of the respective tadpole periods, the effect of treatment appeared earlier in *R. catesbeiana* (see Text-fig. 5). It should be pointed out, however, that tail resorption was carried further in *R. pipiens* (Text-fig. 6) during this time.

The age difference in the groups of tadpoles treated with the same thyroxine concentrations caused no appreciable difference in the growth curves in either species.

The curves obtained for hindlimb growth of tadpoles treated with 1:100,000,000 thyroxine (Text-figs. 3 & 4) are almost identical with that published by Etkin (1935) for thyroidectomized *R. cantabrigensis* tadpoles. Relative to body length, the hindlimbs of the 1:100,000,000 thyroxine-treated animals were longer than normal in both species (Text-fig. 5).



TEXT-FIG. 1. Normal growth curves for (a) body length, (b) tail length, and (c) hindlimb length in *R. pipiens* and *R. catesbeiana*. One unit of age for *R. pipiens* has been made equal to five units for *R. catesbeiana* for easier comparison of the curves.

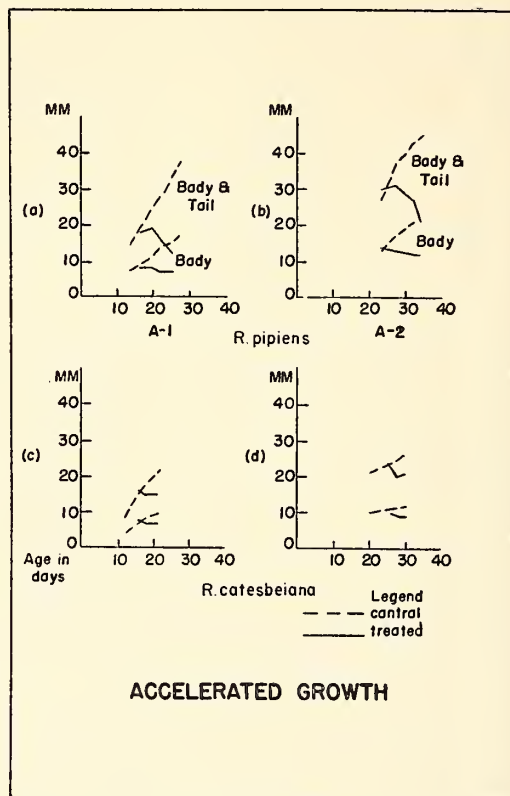
Continuous tail growth of both species of animals treated with 1:100,000,000 thyroxine (Text-fig. 6) was unexpected in view of Blacher's (1928) observation that short exposure to dilute concentrations of thyroidin produced tail shortening.

2. Dissection Results

a. Intestine

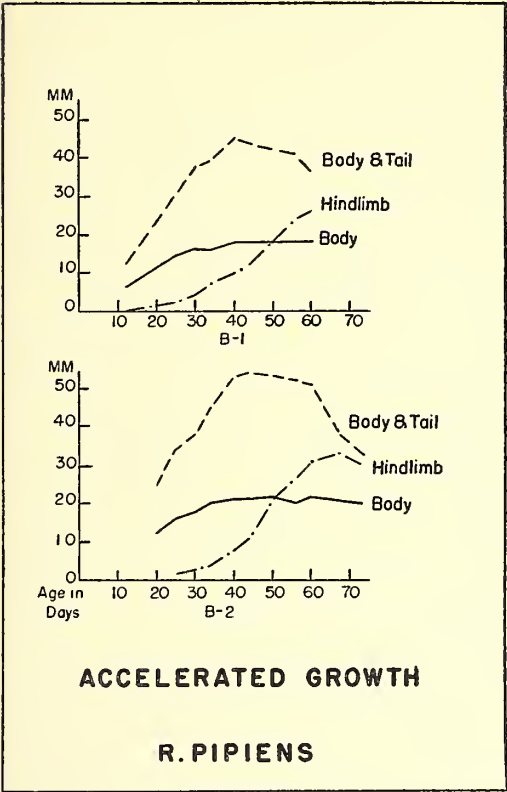
Kuntz (1922) found that the average reduction in intestine length during the normal metamorphosis of *R. pipiens* was 82.2%. In the present investigation the average reduction in the intestine length of control animals was found to be 86.2% for *R. pipiens* and 83.7% for *R. catesbeiana*. These averages are in very good agreement if it is remembered that dietary differences may affect intestine length by as much as 58% (Babak, 1905).

Text-fig. 7a shows the changes in the ratio of intestine length to body length for the normal



TEXT-FIG. 2. Growth under treatment with 1:10,000,000 thyroxine. A-1 curves are for tadpoles treated from 12 days of age; A-2 are for tadpoles treated from 21 days of age; (a) and (b) show data from treated *R. pipiens* tadpoles; (c) and (d) from *R. catesbeiana*.

and for the accelerated *R. pipiens* series; in Text-fig. 7b, comparable data are presented for *R. catesbeiana*. It can be seen that, during normal metamorphosis, the ratio for the tadpole stage is 13 to 14 and it decreases to a value of approximately 2 at the tail resorption stage. By the time of forelimb emergence, one-half of the total shortening had occurred in the intestine of *R. catesbeiana* and three-quarters of the total shortening of the intestine of *R. pipiens* had been effected. Treatment with 1:10,000,000 thyroxine produced shortening of the intestine, giving a ratio (intestine length to body length) of 2; however, shortening had been completed by the forelimb emergence stage. Under the influence of 1:100,000,000 thyroxine, little shortening had taken place by forelimb emergence. By the terminal stage, the intestine length-body length ratio in *R. pipiens* is almost normal as compared with the ratio for *R. catesbeiana* in which the intestine remains considerably longer than twice the body length.

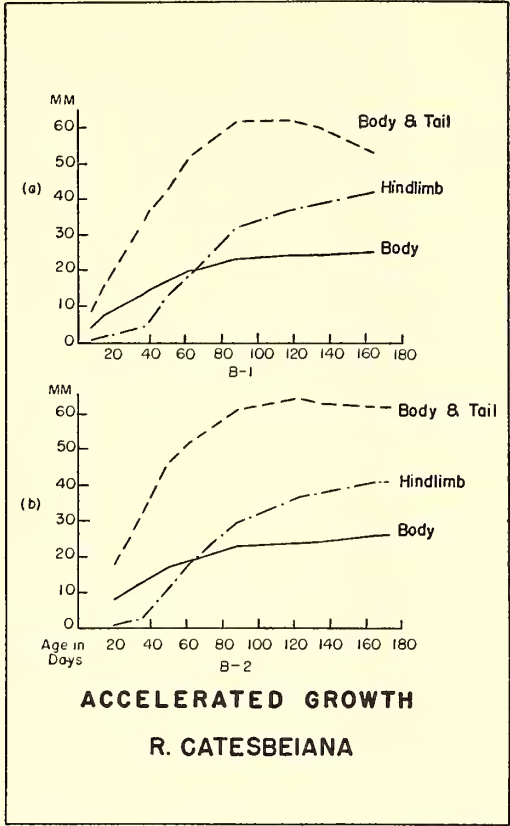


TEXT-FIG. 3. *R. pipiens*, growth of tadpoles under 1:100,000,000 thyroxine treatment. B-1 curves are for tadpoles treated from 12 days of age; B-2 for tadpoles treated from 21 days of age.

Blacher (1928) and Allen (1932) established the order of sensitivity to thyroid treatment of the several tadpole organs. Both Blacher and Allen reported the intestine to be one of the more sensitive organs by virtue of its shortening after even brief periods of exposure to dilute concentrations. In Text-fig. 7, the curves show that the intestine of tadpoles treated with 1:100,000,000 thyroxine continues to grow for some time prior too the onset of shortening. The data can be reconciled if, instead of shortening, one postulates a period of slower intestinal growth in the treated tadpoles than in controls of the same age.

b. Pancreas

In the normal animal the pancreas progressively increases in size up to the time of metamorphosis when regression begins. The shape and the size of the pancreas were the same in treated and in untreated individuals of both species of the same age. Because regression cut short the normal growth period, the experimental animals' pancreas began regression at a

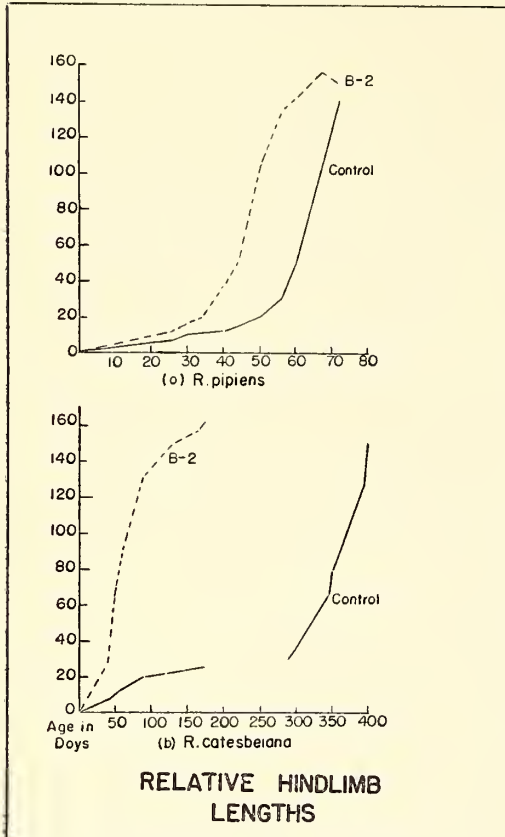


TEXT-FIG. 4. Growth of *R. catesbeiana* tadpoles under 1:100,000,000 thyroxine treatment. (a) B-1 curves are for tadpoles treated from 12 days of age; (b) B-2 curves for tadpoles treated from 21 days of age.

smaller size than normal. Treatment with 1:10,000,000 thyroxine elicited a marked regression at the forelimb emergence stage and further shrinkage was observed in the terminal stage. There was no apparent regression in the pancreas of animals in the forelimb emergence stage which were treated with 1:100,000,000 thyroxine. At the onset of the terminal stage, regression was evident in both species.

c. Gall Bladder

Early in normal development the gall bladder was large as compared with the liver (about 1/5 its size). Later, it was relatively smaller (1/8 to 1/10 of the size of the liver). By the time of forelimb emergence, the gall bladder again appeared larger (1/5 to 1/4 the size of the liver). No measurements were made to show whether these size changes were changes in the gall bladder or in the liver, though it was apparent that the liver first increased and then decreased in size. Hoskins & Hoskins (1919 a & b) reported

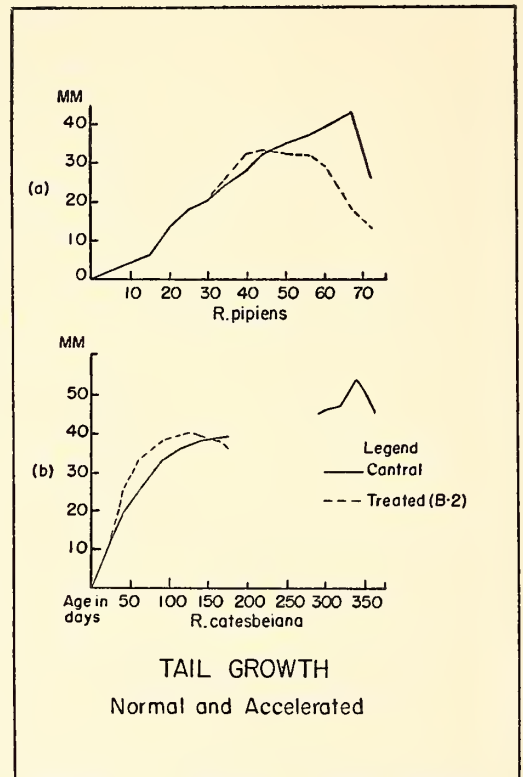


TEXT-FIG. 5. Relative hindlimb lengths in normal tadpoles and tadpoles treated with 1:100,000,000 thyroxine from 21 days of age. (a) *R. pipiens*; (b) *R. catesbeiana*. Age in days is plotted against the ratio of body length to hindlimb up to the tail stub stage in normal animals and to the "terminal" stage in the treated.

that the liver decreased in size during metamorphosis, and Kuntz (1922) reported an 80% reduction in liver weight which took place when tail resorption and intestine reduction were well advanced.

The gall bladders of animals treated with 1:10,000,000 thyroxine remained relatively large. At the terminal stage, they appeared relatively larger than in normal animals at the tail stub stage and the livers appeared to be more than normally reduced in size. The gall bladders of tadpoles treated with 1:100,000,000 thyroxine were still 1/8-1/10 of the size of the liver at the forelimb emergence stage.

Color change in the gall bladder during accelerated metamorphosis was studied in *Hyla versicolor*, *H. crucifer*, *R. clamitans*, *Bufo americanus* and *Ambystoma maculatum* (*A. punctatum* fide Speidel) by Speidel (1926). He noted



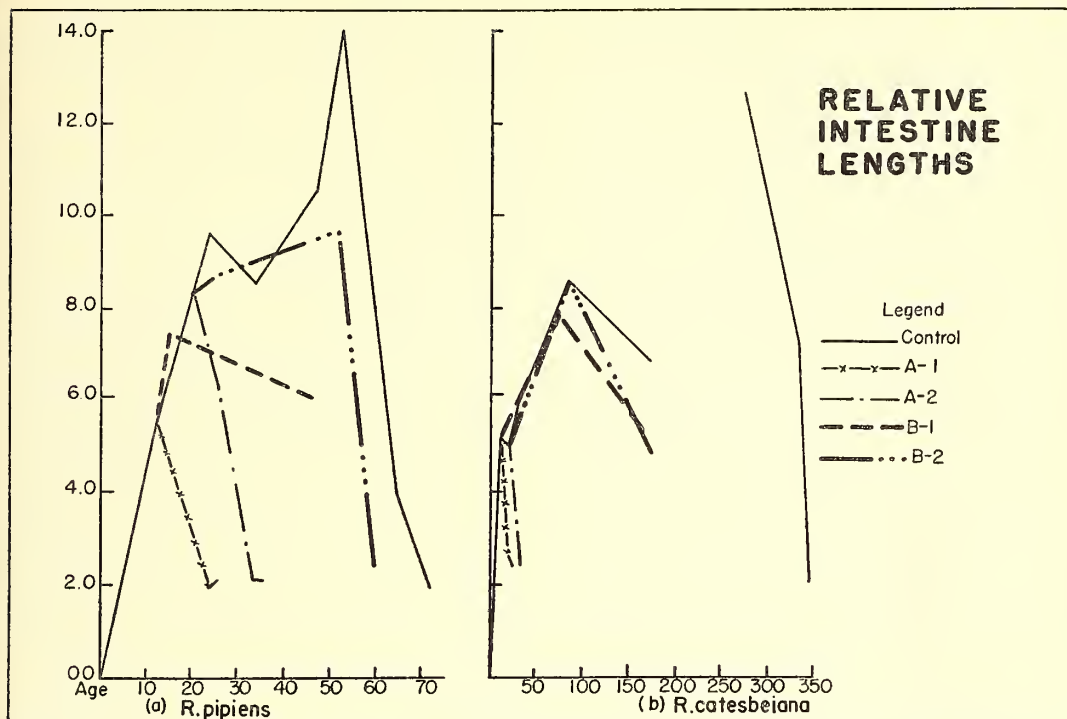
TEXT-FIG. 6. Tail growth in normal tadpoles and tadpoles treated with 1:100,000,000 thyroxine from 21 days of age. (a) *R. pipiens*; (b) *R. catesbeiana*.

no exceptions in several hundred observations from the series: "yellow-green," "brighter-green," "emerald green" and a "very dark green." In normal *R. pipiens*, the gall bladder was dark green at the time of forelimb emergence. In *R. catesbeiana* the gall bladder was emerald green at this time, and it was dark green at the tail stub stage. In most of the 1:10,000,000 thyroxine-treated *R. pipiens* tadpoles, the gall bladder was dark green at the forelimb emergence stage; in *R. catesbeiana*, at the terminal stage, the gall bladder was still emerald green as noted above. In the 1:100,000,000 thyroxine-treated tadpoles of both species, the gall bladder was emerald green at the forelimb emergence stage and approximately half of these individuals had dark green gall bladder at the terminal stage.

d. Urinary Bladder

The urinary bladder developed late in the normal premetamorphic climax period and was small but well developed in the tadpole with fully developed hindlimbs.

At the forelimb emergence stage of both species which had been treated with 1:10,000,000



TEXT-FIG. 7. Relative intestine lengths. Age in days is plotted against the ratio of intestine length to body length for *R. pipiens* in (a) and for *R. catesbeiana* in (b). A-1 curves are for tadpoles treated with 1:10,000,000 thyroxine from 12 days of age; A-2 for those treated with 1:10,000,000 thyroxine from 21 days of age; B-1 for those treated with 1:100,000,000 thyroxine from 12 days of age; B-2 for those treated with 1:100,000,000 thyroxine from 21 days of age.

thyroxine, approximately half had urinary bladders. At the terminal stage, all but one or two animals had small, poorly developed urinary bladders. In both species, the animals treated with 1:100,000,000 thyroxine had well-developed urinary bladders by the time of the forelimb emergence period.

e. Tongue

No measurements of the tongue were made for *R. pipiens*. In *R. catesbeiana*, normal development of the tongue began (when the tadpoles reached 21-27 mm. body length) as a white condensation of tissue in the anterior part of the floor of the mouth. At a body length of 35-38 mm., the tongue was clearly outlined and the tissue mass was about 1 mm. long. At the time of forelimb emergence, the tongue was a well-formed organ, 2.5-3 mm. long, with the posterior edge free and bifurcated. Between the end of forelimb emergence and the onset of the tail stub stage, the tongue grew rapidly and almost doubled its length to 5 mm.

All the experimental animals of both species showed more advanced tongue development than normal animals of the same age. In the

groups treated with 1:10,000,000 which were examined at the terminal stage, the tongue was poorly differentiated, i.e., a free but not bifurcate posterior edge. In the groups treated with 1:100,000,000 thyroxine, the tongue appeared to be the same as in corresponding stages of normal animals. The amount of tongue growth (in length) between the forelimb emergence and the terminal stages for thyroxine-treated *R. catesbeiana* is compared with that in the normal in the table below. Also included is the time in days between the two stages. (The A-1 series, treated with 1:10,000,000 thyroxine from 12 days of age, is omitted because the tongue measured less than 0.5 mm in length at the forelimb emergence stage).

The slower growth rate of the tongue in organisms treated with 1:100,000,000 thyroxine is marked (See B-1 and B-2).

In the normal *R. pipiens* tadpole there are two premetamorphic tongue papillae; in *R. catesbeiana* there are four. These begin to be resorbed in the late tadpole stages and disappear by the onset of tail stub stage. In all the *R. pipiens* series, the papillae were gone by the beginning of the forelimb emergence, but in *R. catesbeiana*,

Stage	TONGUE GROWTH (in mm.)			
	Control	A-2*	B-1**	B-2***
Forelimb Emergence	2.7	0.5	1.3	1.3
Tail Stub (Terminal)	5.0	0.7	2.2	1.8
% Increase	85%	40%	69%	38%
Days between Stages	7	2	82	90

* Treated from 21 days of age with 1:10,000,000 thyroxine.

** Treated from 12 days of age with 1:100,000,000 thyroxine.

***Treated from 21 days of age with 1:100,000,000 thyroxine.

papillae were still present at the terminal stage of animals treated with 1:100,000,000 thyroxine.

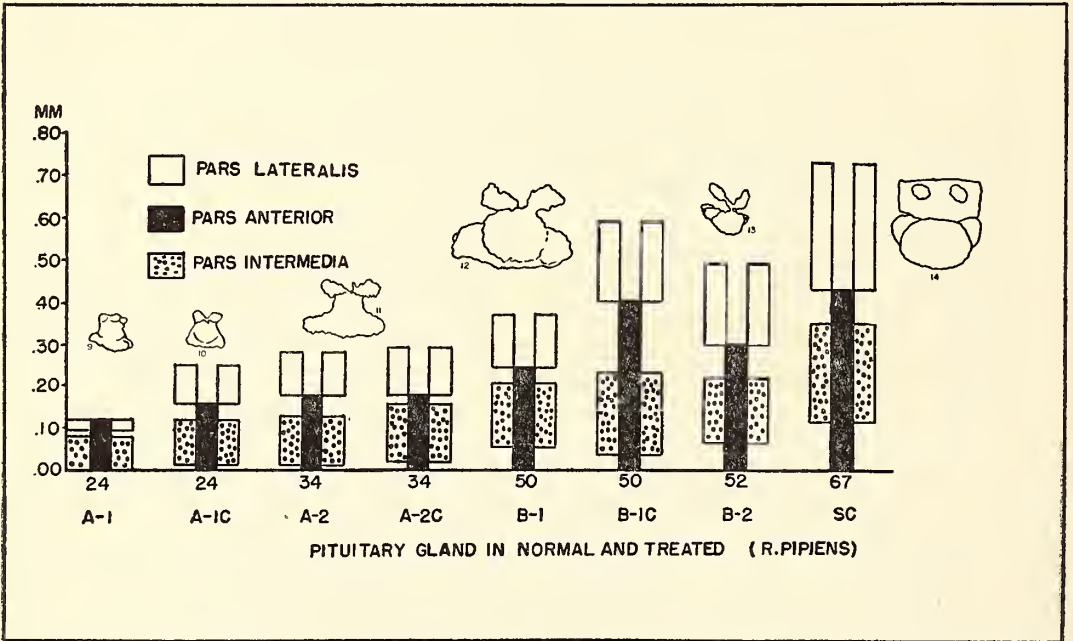
The histology of the premetamorphic tongue papillae of *R. sylvatica* was studied by Helff & Mellicker (1941) who found four papillae, the characteristic number for that species. In their search of the literature, they found that one previous investigator had described these structures. Schulze (1870, cited in Helff & Mellicker,

1941) found two papillae in *Pleobates fusca*, *R. esculenta*, *R. temporaria* and *Bufo cinereus*. *R. catesbeiana* thus resembles *R. sylvatica* in possessing four papillae, whereas *R. pipiens* resembles the species studied by Schulze.

3. Histological Studies: Forelimb Stages, *R. pipiens*

a. Pituitary Gland i. Anatomy

In Text-fig. 8 are reproduced Atwell's (1918) reconstructions of the development of the anuran pituitary gland. It can be seen that two changes take place: first, the two lobes of the pars lateralis come to lie anterior and lateral to and (in the adult) separate from the pars anterior and pars intermedia; second, the mass of the gland grows posteriorly, the Anterior at a more rapid rate than the Intermedia (so that in the adult the former is the most posterior part of the gland. Also in Text-fig. 8, the length of each of the three components of the pituitaries of single normal and experimental animals is plotted in relationship to other parts. These dia-



TEXT-FIG. 8. The pituitary in normal and treated *R. pipiens*. The drawings numbered 9 through 14 above the block graphs are redrawn from Atwell's (1918) reconstructions of pituitary development in Anura. The block graphs show the length and spatial relationships of the pituitary parts of normal and treated *R. pipiens* tadpoles obtained by counting the 10 micra sections each part occupied in each animal. A-1 is data from a forelimb stage animal 24 days old treated with 1:10,000,000 thyroxine from 12 days of age; A-1-C is from an untreated tadpole 24 days old; A-2 is from a forelimb stage animal 34 days old treated with 1:10,000,000 thyroxine from 21 days of age; A-2-C is from an untreated animal 34 days old; B-1 is from a forelimb stage animal 50 days old treated with 1:100,000,000 thyroxine from 12 days of age; B-1-C is from an untreated tadpole 50 days old; B-2 is from a forelimb stage animal 52 days old treated with 1:100,000,000 thyroxine from 21 days of age; SC is from an untreated forelimb stage animal 67 days old.

grams result from plotting the number of 10 micra sections constituting each part of the pituitary.

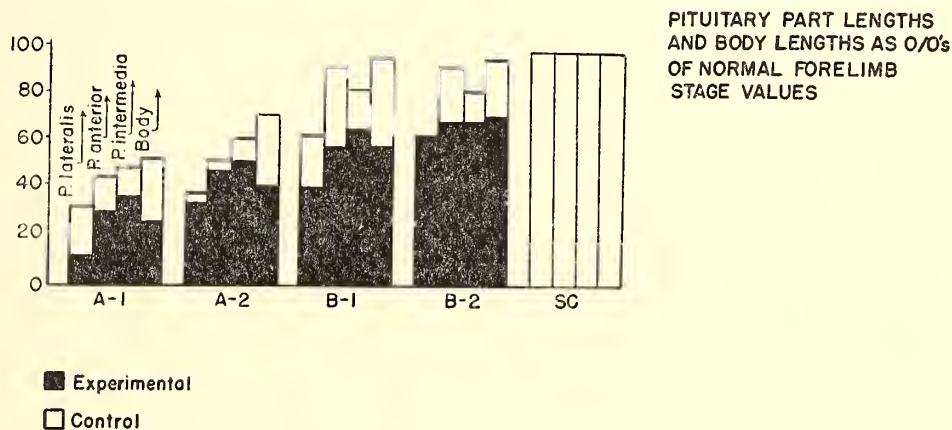
In the 12-day-old, 1:10,000,000 thyroxine-treated forelimb stage (A-1), pituitary relationships correspond to those in Atwell's youngest animal (stage 9), while the untreated animal of the same age (A-1-C) had progressed to Atwell's stage 10. In the 21-day-old, 1:10,000,000 thyroxine-treated forelimb stage animal (A-2), these appear to be the same as in the untreated animal of the same age. Both correspond to Atwell's stage 10 or 11. The higher concentration of thyroxine did not cause precocious anatomical development of the pituitary.

The pituitaries of the animals treated with 1:100,000,000 thyroxine from 12 days of age (B-1) and those treated from 21 days of age (B-2) were smaller than those of either the

normal tadpole of the same age (B-1-C) or of the normal forelimb stage animal (SC). The block graphs do not show the progressive change in the connection between the two lobes of the pars lateralis with the pars anterior illustrated by Atwell's figures 12, 13 and 14. Examination of the slides showed that the normal tadpole (B-1-C), on the basis of lateralis position, had reached a stage between Atwell's 12 and 13 while the normal animal (SC) was between stages 13 and 14. The forelimb animals treated with 1:100,000,000 thyroxine (B-2 and B-4) appear to resemble the normal tadpole more than the normal forelimb emergence stage. The lower concentration of thyroxine, moreover, showed no accelerating effect on the anatomical development of the pituitary.

ii. Relative size

Text-fig. 8 also shows that the pituitaries of



TEXT-FIG. 9. Pituitary part lengths and body lengths of thyroxine-treated forelimb stages compared with those of the normal forelimb stages in *R. pipiens*. The length of each pituitary part and the body length of the experimental forelimb stages and of normal tadpoles of the same age as the treated are shown as percents of the normal forelimb stage values (SC, last set of four 100% blocks). In A-1, data from a forelimb stage animal treated with 1:10,000,000 thyroxine from 12 days of age are shown in black blocks superimposed upon that of an untreated animal of the same age in white. In A-2 the data from a forelimb stage animal treated with 1:10,000,000 thyroxine from 21 days of age are shown in the same way against the data from an untreated tadpole of the same age; B-1 are data from a forelimb stage animal treated from 12 days of age with 1:100,000,000 thyroxine shown against that for an untreated tadpole of the same age; B-2 data from a forelimb stage animal treated from 21 days of age with 1:100,000,000 thyroxine are shown against the data for an untreated tadpole of the same age.

all of the experimental forelimb-emergence animals were shorter than those of untreated animals of the same age. To determine whether the reduced size of the pituitary was proportional to the reduced body size of the thyroxine-treated animals and to determine whether or not all pituitary parts were equally affected, the length of each pituitary part and the body length of the normal forelimb stage animal were taken as 100%. The same measurements for each experimental forelimb animal and for its age control were recalculated as percents of the lengths of the corresponding parts in the normal forelimb animal. In Text-fig. 9, the profiles produced by graphing these values for the experimental animals were superimposed in black upon the profiles of their respective age controls. The last profile to the right (a block of four 100% columns) represents the values for the normal forelimb stage animal.

It can be seen that the bodies of those treated with 1:10,000,000 thyroxine and those treated with 1:100,000,000 thyroxine appeared to have bodies and pituitaries about equally inhibited (with regard to length) at the forelimb stage, and in these animals the pars anterior appeared to be the pituitary component most inhibited.

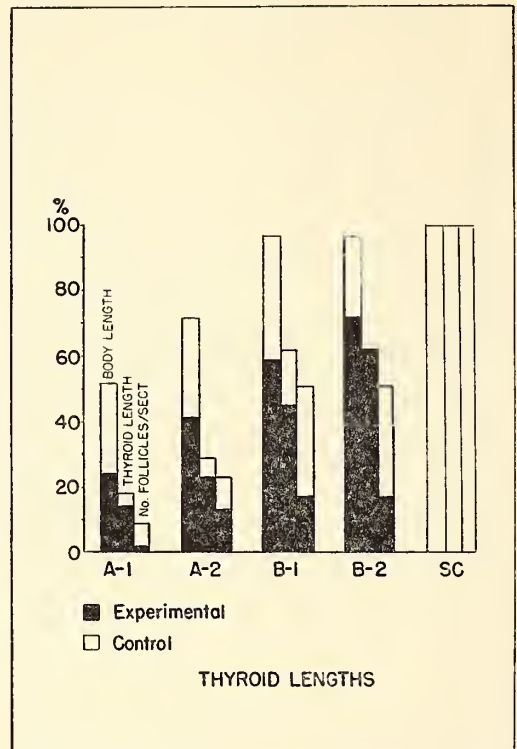
iii. Cellular Differentiation

Distribution and differential counts of the pituitary cell types were not considered because of the thickness of the sections. The cytoplasm in the cells of all the lobes was less abundant in the experimental animals than in either the age controls or the normal forelimb stage. Pigment granules which were large and coarse in young normal stages were more evident in all the experimental than in the stage controls.

b. Thyroid Gland

i. Size of the Gland

Conclusions as to thyroid size were based on the length of the glands determined by counting the number of 1 micra sections which the two halves of the gland occupied in each animal, and on a relative area per section derived from counting the number of follicles containing visible colloid. To show how the thyroids of the thyroxine-treated forelimb stage animals differed from those of the normal forelimb stage animal and from the untreated tadpoles of the same age, body length, length of thyroid and average number of colloid-filled follicles per section in the normal forelimb stage animal were arbitrarily rated as 100%. The same data for the treated animals (forelimb stage) and for their respective age controls were recalculated as percents of these norms. In Text-fig. 10 are five profiles resulting from this treatment of the data. At the extreme right is the normal forelimb stage pro-



TEXT-FIG. 10. Thyroid size and body size in normal and thyroxine-treated *R. pipiens*. Body length, length of thyroid determined by counting the number of 10 micra sections the gland occupied and the average number of follicles per section for the accelerated forelimb stages and for untreated animals of the same ages as the treated are shown as percents of the normal forelimb stage values (SC, the last set of three 100% blocks). The values for each treated forelimb stage animal are shown in black blocks superimposed on the same values for a normal tadpole of the same age shown by white blocks. A-1 shows the values for a forelimb stage animal treated from 12 days of age with 1:10,000,000 thyroxine and for a normal animal of the same age; A-2, for a forelimb stage animal treated from 21 days of age with 1:10,000,000 thyroxine and for a normal tadpole of the same age; B-1 for a forelimb stage animal treated from 12 days of age with 1:100,000,000 thyroxine and for a normal tadpole of the same age; B-2 for a treated forelimb stage animal treated from 21 days of age with 1:100,000,000 thyroxine and for a normal tadpole of the same age.

file. To the left are the profiles for the untreated tadpoles. Superimposed upon these are the profiles of the treated forelimb stage animals of the same age.

Text-fig. 10 shows that the thyroids of the treated animals at the forelimb emergence stage were inhibited as reflected by their size when compared with the normal forelimb stage and

untreated animals of the same age. Inhibition as indicated by area (determined by the number of follicles) was greater than that indicated by length.

ii. Mitotic Activity

In the following table are given the number of 10 micra sections occupied by both the right and left halves of the thyroid glands, and the number of mitoses in the entire glands.

	Sections	Mitoses
A-1	30	3
A-1-C	39	47
A-2	49	12
A-2-C	62	120
B-1	95	14
B-1-C	130	406
B-2	131	24
SC	211	861

The normal series—A-1-C, A-2-C, B-1-C and SC—gave evidence of higher mitotic activity than did the treated animals.

iii. Glandular Activity

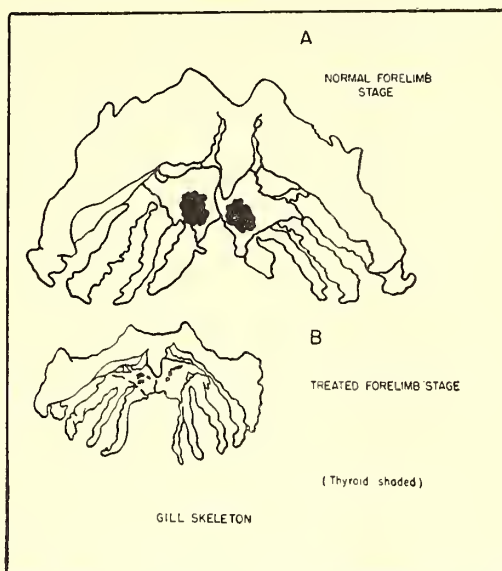
A thyroid gland made up of vacuolate columnar cells, with vacuolate colloid, and of many collapsed follicles, possesses the generally accepted histological criteria of a physiologically active gland. The forelimb stage animals treated from 12 days of age with 1:10,000,000 thyroxine (A-1) had thyroid glands made up of cuboidal cells with scant cytoplasm, with few follicles, and with no vacuolation. In those treated with 1:100,000,000 thyroxine from 21 days of age (A-2), the thyroid cells were cuboidal. The cells had more cytoplasm than those of the A-1 animals but less than those in animals of the same age. As in the age controls, a few follicles showed vacuolation of the colloid. The animals from both age groups treated with 1:100,000,000 thyroxine had thyroids in which the cuboidal cells were approaching a columnar architecture. The thyroids of the normal forelimb stage animals bore all of the criteria of high activity.

iv. Pigment

In the younger normal animals (as was noted by D'Angelo & Charipper, 1939) large aggregates of pigment are conspicuous features of the thyroid gland. By the time of forelimb emergence, however, such aggregates were rare. Moreover, the granules are distributed and the pigmentation is not conspicuous. All of the experimental animals showed pigmentation either to the same degree or to a greater degree than their respective age controls.

v. Thyroid Position

Text-fig. 11 shows outline drawings from



TEXT-FIG. 11. Thyroid position relative to the gill skeleton in the normal forelimb stage and in the forelimb stage produced by treatment with 1:100,000,000 thyroxine from 12 days of age. Graphic reconstruction from serial sections. Normal stage magnified 5 \times ; treated 11.25 \times . The thyroid is shaded.

graphic reconstruction of the thyroid gland and its relationship to the ventral aspect of the hyobranchial cartilages. Text-fig. 11a shows the normal forelimb emergence stage (5 \times). Text-fig. 11b is the forelimb emergence stage after 1:100,000,000 thyroxine treatment from 12 days of age (enlarged 11.25 \times). The thyroid gland assumed a more anterior position under the gill-bearing skeleton in the treated animals than in the normal. D'Angelo & Charipper's (1939) Figure 1, illustrating the normal changes in thyroid position up to and including metamorphosis, indicates that the more anterior position is characteristic of normal tadpoles of the same age as the treated. The position of the thyroid in the normal forelimb stage agrees with their observations from the same stage. Thus 1:10,000,000 thyroxine treatment did not effect a precocious migration of the thyroid.

c. Small Intestine

In the normal forelimb stage animal, the histology of the small intestine is well-represented by Kuntz's (1922) figures for the same stage of *R. pipiens* and by Jane's (1934) illustration for this stage in thyroid-fed tadpoles of *R. clamitans*. There were many mitoses in the basal cells of the new mucosal layer. The old mucosa was evidenced by conspicuous necrotic masses. The submucosa and muscularis had

thickened considerably. The forelimb stage animals treated with 1:10,000,000 thyroxine had the intestinal histology of the normal forelimb stage. However, the cytoplasm of the cells in all layers was very scant and the resulting histology was superficially quite different from the normal. Forelimb stage animals treated with 1:100,000,000 thyroxine had the same intestinal histology as that of the untreated tadpoles of the same age.

d. *Pancreas*

In the normal forelimb stage animal regression of the pancreas was far advanced. The histological picture represented a condition intermediate to Kaywin's (1936) stages 3 and 4 of thyroxine-treated *R. catesbeiana*. The acini showed three stages of metamorphic changes: (1) some were necrotic, (2) some were made up of syncytial cells, and (3) some were made up of cells with large nuclei and sparse, deeply-staining cytoplasm. There were pronounced connective tissue spaces.

In the forelimb stage of animals treated with 1:10,000,000 thyroxine, the pancreas was comparable to the normal forelimb stage pancreas as regards the degree of metamorphic change. However, pigment was very conspicuous. Forelimb stage animals treated with 1:100,000,000 thyroxine failed to show metamorphic change in the pancreas. The glands were smaller than those of the untreated tadpoles of the same age, but there were no signs of loss of definition of cell boundaries or necrosis in the acinar cells.

e. *Summary of Observations on the Histology of the Forelimb Stages of R. pipiens*

Kahn (1916) found that the pituitaries of tadpoles treated with horse thyroid were much larger than normal. Schliefer (1935) found that thyroid extract had no effect on the pituitary although the development of the gland was accelerated along with the rest of the body. Under the conditions of the present study the anatomical development, at the forelimb emergence stage, of the pituitary of thyroxine-treated animals was not found to be more advanced than that of untreated animals of the same age. In fact, the glands were smaller. Treatment with 1:10,000,000 thyroxine was less inhibitory to pituitary growth than it was to body growth. Thus, in agreement with Kahn, the pituitaries were larger than those of untreated tadpoles of the same age. After treatment with 1:100,000,000, body size and pituitary size were in a more normal proportion; with this concentration, the pars anterior appeared to be more inhibited than the other pituitary components. With both concentrations, the cytoplasm of the cells of all parts of the pituitary gland was sparse and pig-

ment remained conspicuous in the pars anterior and pars lateralis.

The thyroids of treated animals showed evidence of inhibition in every respect considered at forelimb emergence. They were much smaller, had a lower mitotic rate and give histological evidence of a lower degree of differentiation and physiological activity than the glands of either the normal forelimb stage or of the untreated tadpoles of the same age. These findings agree with those of Clements (1932), Etkin (1935) and Brinks (1936).

The small intestine and pancreas in animals treated with 1:10,000,000 thyroxine showed the same type of histological change at the time of forelimb emergence as that of normal animals at the same stage. On the other hand, the intestines and pancreases of those treated with 1:100,000,000 thyroxine did not show metamorphic change.

4. *General Summary of Observations*

A comparison of the condition of seven internal organs, in normal metamorphic stages and in comparable stages produced by treatment with two concentrations of thyroxine, has shown that at each stage, the accelerated animals are different not only from the normal but also from each other. This is summarized, in the table below, for the forelimb stage.

Difference in the length of the tadpole period in *R. pipiens* and in *R. catesbeiana* did not greatly affect the results of thyroxine treatment as studied by growth measurements and dissection. *R. catesbeiana* reacted earlier, considering its normal tadpole period, to both concentrations of thyroxine than did *R. pipiens*. In days, *R. catesbeiana* reacted more quickly to 1:10,000,000 thyroxine and less quickly to 1:100,000,000 thyroxine than *R. pipiens*. As judged from the degree of response, *R. catesbeiana* was less sensitive than was *R. pipiens*, as shown by the fact that resorption of the tail and shortening of the intestine after 1:100,000,000 thyroxine treatment was not as advanced. In comparison with their respective normal stages, nevertheless, the animals showing accelerated development behaved similarly in both species.

DISCUSSION

The thyroid glands themselves of animals undergoing thyroxine-accelerated metamorphosis apparently do not modify the effects of thyroxine treatment. Etkin (1935) reached this conclusion by comparing the effects of thyroxine on thyroidectomized and partially thyroidectomized *R. cantabrigensis* tadpoles. The present study supports that conclusion by the detailed similarity of the external metamorphosis of acceler-

NORMAL DEVELOPMENT IN NORMAL AND TREATED FORELIMB STAGE ANIMALS

	NORMAL	THYROXINE-TREATED		AGE CONTROLS FOR (1) and (2)
		(1) 1:10,000,000	(2) 1:100,000,000	
1. Intestine				
a. Shortening	$\frac{3}{4}$ - <i>R. pipiens</i> $\frac{1}{2}$ - <i>R. catesbeiana</i>	Complete	Little or none	None
b. Histology (<i>R. pipiens</i>)	Tadpole & adult	Tadpole & adult	Tadpole	Tadpole
2. Pancreas				
a. Regression	Evident	Excessive	Not evident	None
b. Histology (<i>R. pipiens</i>)	Tadpole & adult	Tadpole & adult	Tadpole	Tadpole
3. Gall Bladder				
a. Relative size (relation to liver)	$\frac{1}{6}$ - $\frac{1}{4}$	$\frac{1}{4}$ - $\frac{1}{3}$	$\frac{1}{8}$ - $\frac{1}{10}$	$\frac{1}{8}$ - $\frac{1}{10}$
b. Color	Emerald (<i>R. catesbeiana</i>) Dk. green (<i>R. pipiens</i>)	Emerald Dk. green	Emerald	(1) Yellow-green (2) Pale green
4. Urinary Bladder	Well-formed	None in $\frac{1}{2}$; poorly developed in $\frac{1}{2}$	Well-formed	None
5. Tongue				Tissue condensation in (1); well-formed in (2)
a. Shape	Well-formed	Immature	Well-formed	2 present in <i>R. pipiens</i>
b. Premetamorphic Papillae	Regressive	Gone (<i>R. pipiens</i>) Regressive (<i>R. catesbeiana</i>)	Gone Regressing	4 present in <i>R. catesbeiana</i>
6. Pituitary (<i>R. pipiens</i>)				
a. Anatomy	Atwell's stage 13-14	Atwell's stages 9 and 10	Atwell's stage 12 or 13	Stage 10 and 11 for (1) Stage 12 or 13 for (2)
b. Size				
i. Relative to age norm		Smaller	Smaller (especially pars anterior)	
ii. Relative to body size		Larger than normal	About normal	
7. Thyroid (<i>R. pipiens</i>)				
a. Size	Large	Very small	Small	Increasing
b. Histology	Climax	Retarded	Retarded	Many
c. Mitoses	Many	Few	Few	—
d. Position	Migrating	Not migrating	—	—

ated intact *R. pipiens* and *R. catesbeiana* to that of his accelerated, thyroidectomized animals. The development of the thyroids of treated *R. pipiens* at the time of forelimb emergence was very much inhibited and resembled that of hypophysectomized tadpoles described by Atwell (1935) seventeen months after operation. The growth of the pituitaries of these animals was also inhibited. D'Angelo (1941) correlated the growth and differentiation of the thyroid with the marked growth and basophilic differentiation of the pituitary pars anterior during the period of rapid hindlimb growth. Inhibited pituitary development is a plausible explanation for the inhibited condition and apparent inactivity of the thyroids of thyroxine-treated tadpoles.

In attempting to duplicate the normal pattern of sequence and spacing of the external metamorphic events, Etkin (1935) found that no one concentration of thyroxine could effect this result. However, by starting with low concentrations and gradually increasing the dosage, he obviated both the simultaneous occurrence of events normally spaced in time which resulted from the use of single high concentrations and the greater than normal intervals between events which resulted from the use of single low concentrations. Schreiber (1934 a & b) and Gache (1940) account for both the sequence and the spacing of events in normal metamorphosis as results of differences in the response thresholds of the several organs at the level of thyroxine increases. Etkin, having found the sequence of events unchanged by different concentrations of thyroxine, considered that this sequence was inherent in the tissues, all of which were sensitive even to the lowest concentrations, and concluded that only the spacing of events and rate of response were thyroxine controlled.

If the sequence of events is controlled by increasing concentrations of hormone reaching successively the low thresholds of early events and the higher thresholds of later events, then a particular concentration capable of initiating, let us say, a late event must also be able to initiate other events normally occurring earlier or at the same time. If the sequence of events is inherent in the tissues and is independent of the concentration of thyroxine, then if a particular event has already taken place in both normal and accelerated animals, other events already begun in normal animals should also have begun in the accelerated animals regardless of the concentrations used.

In the present experiments, normally metamorphosing and accelerated animals were examined at a time when, in each, the same external metamorphic event had just occurred,

namely, forelimb emergence. In the normal animal, the histology of the intestine and pancreas is midway in the change to the adult condition. In animals treated with 1:100,000,000 thyroxine, there was no histological change apparent in either organ, while those treated with 1:10,000,000 thyroxine resembled the normal in histology. The urinary bladder is absent in half the forelimb stage animals treated with 1:10,000,000 thyroxine, but it is present in the normal forelimb stage, the normal late tadpole, and in the 1:100,000,000 thyroxine-treated animals in the forelimb stage. The gall bladders of 1:100,000,000 thyroxine-treated animals retain the tadpole size relation to the liver, but in the normal forelimb stage and in the 1:10,000,000 thyroxine-treated forelimb stage, the gall bladders are increased in size relative to the liver.

If the delayed events cited were just begun although not far advanced, then these deviations in the accelerated animals from the normal integration of events could be explained as concentration effects upon the reaction rates and, thus, upon the spacing of events, rather than as an alteration of sequence. This would corroborate Etkin's views. Despite the difficulty imposed by the conditions of the present experiments in ascertaining precisely the initiation of an internal metamorphic event, the probability of its having occurred in normal sequence regardless of the thyroxine concentration can be further explored if its position as one of a sequence of three events is followed.

In normal animals, the urinary bladder (1) is well formed and intestinal shortening (2) is $\frac{1}{2}$ to $\frac{2}{3}$ complete when the forelimbs emerge (3). In 1:100,000,000 thyroxine-treated animals, the urinary bladder (1) is well formed at forelimb emergence (3) but there has been little or no shortening of the intestine (2). In 1:10,000,000 thyroxine-treated tadpoles, all have fully shortened intestines (2) at forelimb emergence (3) but half have no urinary bladders (1). At any given moment in normal metamorphosis, the rising concentration of thyroxine is the same for all organs and although, as Etkin suggests, each event may have its own rate to be speeded or retarded by concentration, this rate at normal concentrations is necessarily related to those of other events taking place at the same time. If all the events were initiated in the natural sequence in the development of the animals treated with the two concentrations, the cited deviations in developmental pattern from the normal in the two groups can be ascribed entirely to the effects of the experimental concentrations on rate. It seems improbable that the urinary bladder, normally formed before intes-

tinal shortening begins, should not be visible under 17 \times magnification in half the 1:10,000,000 thyroxine-treated animals at the forelimb stage, all with fully shortened intestines, unless the beginning of its development had been delayed relative to the natural or normal developmental sequence.

If the normal sequence of events is not a matter of successive threshold responses (since a concentration that produced one event did not produce all the other naturally concurrent events) and is not independent of thyroxine concentration (since both concentrations apparently produced altered sequence), another explanation for the control of metamorphic sequence must be sought.

The lack of significant differences in response to the same thyroxine concentrations in the two species studied indicates that differences in tissue sensitivity are not the cause of the species differences in the length of time before the onset of metamorphosis. This, taken with the precocious thyroid activity and metamorphosis produced by Ingram (1928) in *R. catesbeiana* with *R. clamata* pituitary implants; with Etkin's (1950) demonstration of tissue sensitivity to thyroxine as early as the opercular closure stage; and with the well-known effects of hypophysectomy on metamorphosis, leads to the conclusion that the onset of metamorphic change is pituitary-controlled. It has been accepted that this control is exerted through trophic action on the thyroid gland. If the sequence of metamorphic events is neither solely an effect of the thyroid in producing rising thyroxine concentrations nor independent of concentration and inherent in the tissues, perhaps the control of metamorphic sequence may be found in a thyroid-pituitary interrelationship at the tissue level.

It is evident that a dynamic equilibrium must be maintained between growth and differentiation during the late tadpole and early metamorphic period. Tadpole organs continue to grow up to the time the changes take place which cause them either to disappear or differentiate, producing the adult condition. Potential adult organs both grow and differentiate during the tadpole period. That both the thyroid and pituitary are involved has been shown in the results of hypophysectomy and thyroidectomy. Smith (1916 a & b, 1918) showed that although the initial growth rates of normal and hypophysectomized tadpoles were very similar, a definite retardation of growth became evident in the second half of the tadpole period during which growth is normally rapid. Thus, the effect of the pituitary upon growth begins to be exerted at the period of rapid thyroid, hindlimb and general body growth. Hoskins & Hoskins (1919

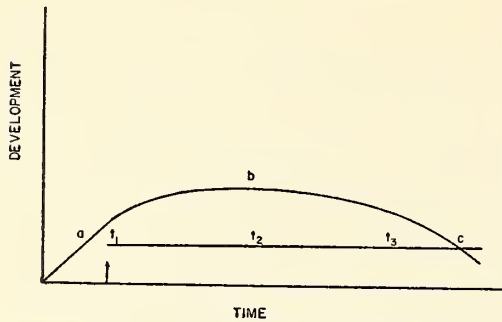
a & b) found that thyroidectomized tadpoles grew more rapidly and were almost twice the size of normal animals at the time they should have metamorphosed. Gordon, Goldsmith, & Charipper (1943, 1945) also reported excessive growth in chemically thyroidectomized tadpoles. These results suggest that, after an initial independent period, growth during the second part of the tadpole period is affected by two factors: (1) a factor from the pituitary-promoting growth and (2) a factor from the thyroid-inhibiting growth. That the latter normally overtakes the former may be inferred from the cessation of growth at metamorphosis when thyroid activity is at its peak. It is of interest to note here that in accelerated metamorphosis, in an organ like the pancreas which normally develops a typical structure that is replaced by a different adult structure at metamorphosis, the acceleration does not consist of a telescoping in time of the normal anatomical history of the organ. Instead, the tadpole part is dropped out. The initiation of metamorphic sequence may depend upon a succession of tissue-determined critical ratios between the concentrations of the pituitary growth factor and thyroxine.

In an early period, the initiation of development in adult organs might take place in an order determined by the concentration of thyroxine and the growth stimulus, while tadpole organs unaffected by the low thyroxine inhibition continue to grow; in an intermediate period, growth of all organs continues followed by a later period in which growth slows in all organs and as the growth/thyroxine ratio changes, successive tadpole organs begin metamorphosis.

This explanation, based on the growth curves shown in Text-fig. 2 and applied to the conditions under 1:10,000,000 thyroxine treatment, might be present as follows.

Because the experiments began in the period which Smith found independent of hypophysectomy, the cessation of growth observed would indicate that pituitary independent growth is also inhibited by thyroxine in this concentration. Tadpole growth rapidly ceased, regressive changes were marked, and adult organs appeared but were small and underdeveloped. The pituitary and thyroid were retarded compared with the glands of untreated tadpoles of the same age.

In the 1:100,000,000 thyroxine experiments, tadpole growth continued. At first, this was a virtually normal rate, but as time went on the growth curves flattened. The conditions in 1:100,000,000 thyroxine acceleration might be represented as follows (Text-fig. 12). Here "a" is the period of pituitary independent growth,



TEXT-FIG. 12. For explanation see text below.

"b" is growth affected by 1:100,000,000 thyroxine ("c") applied from the time indicated by the arrow. Three different periods in the relationship of "a"—"b" to "c" can be recognized, but each differs from the corresponding period in the "normal" diagram. In period t_1 , 1:100,000,000 thyroxine is applied; the growth rate increases whereas the level of thyroxine does not. The thyroxine concentration is too low to stop tadpole growth, but is sufficient to initiate the growth of the adult organs.

In period t_2 , the relation of "b" and "c" is fairly constant, as can be seen (Text-fig. 12). In period t_3 , "b" decreases slowly and "c" remains constant. As a result "b" approaches "c" more slowly and the period t_3 is longer. This lateration in the amount of change and the timing of the change in the growth/thyroxine relationship could account for the relatively longer limbs of the 1:100,000,000 thyroxine-treated animals, the slower-than-normal tail resorption and the delay in intestinal shortening. That tail resorption eventually takes place in some specimens, as does intestinal shortening, can be explained by the growth factor falling slowly in value to a point where, although the thyroxine concentration has not been changed, the normal "critical" ratio between the two factors is approached. This would also bring Allen's (1932) statement that "an apparently subminimal concentration of thyroxine may be effective if it acts long enough" into conformity with subsequent evidence that thyroxine is not stored in the tissues (Etkin, 1935).

Experiments on starved tadpoles have produced results of great interest in this connection. D'Angelo, Gordon & Charipper (1938) showed that starvation imposed before the 5-8 mm. hindlimb stage in *R. sylvatica* retarded development and resulted in failure of metamorphosis, but starvation imposed after this resulted in precocious metamorphosis. Later it was found (1941) that early starvation resulted in extreme retardation of the thyroid gland and failure of

cell differentiation in the pituitary. Tadpoles starved at later stages had thyroids which showed secretory activity for some time. It was suggested that early metamorphosis may be the result of precocious thyroid activity possible from the increased sensitivity to thyrotrophic hormone. There is also a possibility that once the thyroid secretes hormone, a reduction in the growth potential by starvation could precipitate metamorphosis at a level of thyroxine production which would be insufficient normally. It may be necessary to point out that the smaller body size of the 1:100,000,000 thyroxine-treated animals in the present experiments is not the result of starvation from precocious cessation of feeding. The intestines were distended with food when examined histologically at the forelimb stage and feces were abundantly present in the thyroxine solutions at the daily changes until well after this period.

The explanation above has been offered to show how the normal sequence of metamorphic events might be controlled by a series of critical ratios between the growth-promoting influence of the pituitary and the effects of the thyroid. The experimental data offer little evidence concerning the function of the pituitary-accelerated metamorphosis. The pituitary glands were smaller than normal, on an absolute basis, in the treated animals but not relatively, as compared with body size. The pars anterior seemed to be more reduced than the other parts. The anatomy was tadpole rather than normal at the forelimb stage. The appearance of the thyroid indicated deficiency of thyrotrophic hormone. On such evidence elaboration of theory is premature and must await further data such as might be afforded, for example, by a comparison of the effects of thyroxine treatment on metamorphic sequence in intact and in hypophysectomized tadpoles.

SUMMARY

1. Comparison of the development of the intestine, pancreas, urinary bladder, tongue, gall bladder, pituitary and thyroid glands in normal and thyroxine-accelerated *R. pipiens* and *R. catesbeiana* tadpoles at similar metamorphic stages has shown that the accelerated animals differ from the normal and that those accelerated by 1:10,000,000 thyroxine were different from those accelerated by 1:100,000,000.

2. In the same animals, different organs showed either the same or more advanced development than did the corresponding organs of normal animals.

3. Treatment of *R. pipiens* tadpoles with either concentration resulted in less developed thyroids and pituitaries than were found in

naturally metamorphosed animals of the same stage.

4. The responses of the tadpoles of the two species to the same experimental treatment were much alike in every point compared despite the difference in the length of their tadpole periods.

5. The data fail to support the theory that the sequence of metamorphic events is dependent upon a series of thyroxine thresholds in the several organs, but indicate some probability that the sequence is dependent in part on thyroxine concentration.

6. It is suggested that normal metamorphic sequence may result from a thyroid-pituitary relationship which changes with time and operates at the tissue-cellular level rather than at the organ level.

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On the Bramid Fishes of the Gulf of Mexico¹

GILES W. MEAD²

(Plates I-III)

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I. INTRODUCTION

BERG (1947: 474) includes the Pteraclidae and Steinegeriidae within the Bramidae. Although this arrangement may be a natural one, it is convenient here to follow the older classifications (*e. g.* Jordan, 1923: 181) and restrict the family to the genera *Brama*, *Taractes*, *Collybus* and *Eumegistus* and their synonyms. The Pteraclidae can be separated from the Bramidae by the longer bases and more anterior origins of their vertical fins. The Steinegeriidae includes only *Steinegeria rubescens* Jordan & Evermann (1887) of which only the type is known. This specimen was collected from the stomach of a red "grouper" which was caught in the Gulf of Mexico off Pensacola, Florida. It is in poor condition. Although the systematic position of this fish has not been established, its nearly vertical mouth, non-falcate dorsal and anal fins, the enlarged spines of the caudal peduncle and its nearly flat forehead separate it from *Taractes*, *Collybus* and *Brama* of similar size. *Steinegeria rubescens* will be the subject of a later paper, but is excluded from further comment here. A revision of the major classification of the bramid-like fishes is needed as badly as an analysis of the species and of the allometric growth associated with each.

The family, as so restricted, is represented in

the Gulf of Mexico by two species: *Collybus drachme*, reported here for the first time from five off-shore localities; and a species of *Taractes* which I have called *T. longipinnis* and which is also first recorded here from the Gulf of Mexico. Although my material is inadequate for an analysis of the non-Gulf bramids, I have reviewed some of these in order to more clearly establish the identity of these Gulf of Mexico specimens.

"Length" as used here refers to standard length unless otherwise qualified. All measurements over 100 mm. were made with dividers and recorded in millimeters. Measurements between 5 and 100 mm. were made with dividers or dial calipers and recorded in half millimeters. Measurements of less than five mm. were taken with a calibrated ocular grid micrometer and were recorded to the nearest tenth of a millimeter.

II. MATERIAL AND ACKNOWLEDGEMENTS

The first Gulf bramid which came to my attention was a *Taractes* 74.0 mm. in standard length (85 mm. fork length) taken by the U.S. Fish and Wildlife Service vessel *Oregon* at station no. 1043, an experimental tuna long-line station occupied on May 11, 1954, at Lat. 24° 16' N., Long. 92° 00' W. The specimen was found in the stomach of a yellowfin tuna (*Neothunnus albacares*) which was caught at a depth of less than 35 fathoms. The superficial fin membranes had been largely digested and some of the scales, head bones and fin rays were damaged, but the fish was otherwise in good condition.

Four adult *Taractes* were caught on later *Oregon* cruises. All were taken by the long-line at depths less than 35 fathoms. These specimens, 376, 371, 357 and 349 mm. in standard length (418, 413, 394 and 390 mm. in fork length respectively), came from the following two *Oregon* stations:

¹Contribution No. 973, Department of Tropical Research, New York Zoological Society.

²Ichthyological Laboratory U. S. Fish and Wildlife Service, U. S. National Museum, Washington 25, D. C.

1173 28° 54' N. Lat., 88° 02' W. Long.,
August 25, 1954

1317 28° 23' N. Lat., 88° 43' W. Long.,
June 11, 1955

Three of these fish are now in the collections of the U.S. National Museum, where they bear the catalogue numbers US 157793 and US 164328. These specimens, and the types of *Collybus drachme* and *Steinegeria rubescens*, were made available by Dr. Leonard P. Schultz, Curator of Fishes.

Ten juvenile specimens of *Collybus drachme* were collected at the following Oregon stations:

1043 24° 16' N. Lat., 92° 00' W. Long.,
May 11, 1954

1065 20° 34' N. Lat., 95° 37' W. Long.,
May 21, 1954

1377 27° 43' N. Lat., 88° 43' W. Long.,
August, 1955

1484 20° 50' N. Lat., 95° 53' W. Long.,
April 3, 1956

1486 22° 25' N. Lat., 97° 00' W. Long.,
April 4, 1956

I am indebted to Stewart Springer and Harvey R. Bullis, Jr., of the U.S. Fish and Wildlife Service, Pascagoula, Mississippi, and Edgar L. Arnold, Jr., of the U.S. Fish and Wildlife Service, Galveston, Texas, for the original preservation of this Oregon material.

G. E. Maul, Curator of Fishes in the Museu Municipal do Funchal, Funchal, Madeira, has kindly sent information regarding *Taractes* from Madeiran waters, and Dr. E. H. Bryan, Jr., Curator of Collections in the Bishop Museum, Honolulu, has sent a photograph of a cast of *Collybus drachme*.

Comparative bramid material from the Bermuda collections of Dr. William Beebe is now deposited in the Natural History Museum of Stanford University and was made available by Dr. George S. Myers.

The large *Taractes* from Nova Scotia which was reported by Bigelow & Schroeder (1929; MCZ no. 31598) and a photograph of a 570 mm. (fork length) Portuguese *Taractes* sent to these authors by Dr. Alfredo Ramalho were made available by Drs. Henry B. Bigelow and William C. Schroeder of Harvard University and the Woods Hole Oceanographic Institution.

III. *Taractes longipinnis*

Since my study of the six western North Atlantic *Taractes* listed above indicates that they are specifically identical regardless of certain differences among them, it is necessary to describe the more striking similarities and differences among the individuals of this series.

A 357 mm. Gulf specimen (Pl. I, Fig. 1) was

first compared with the 618 mm. fish reported by Bigelow & Schroeder (1929) from Cape Sable, Nova Scotia. These fish differ in several respects. In the smaller fish the ventral fins originate under the middle of the bases of the pectoral fins, while in the Nova Scotia specimen their origins are beneath the anterior edges of the pectoral bases. The 357 mm. specimen also has relatively longer dorsal and anal lobes than the 618 mm. specimen, but, as Barnard (1948: 357) has suggested and as will be more fully discussed below, a progressive relative shortening of these fin lobes accompanies an increase in length of the adult fish. The 357 mm. individual also differs in having spines on the posterior body scales, and its eye is a little smaller and more nearly circular than that of the larger fish. Differences such as these accompany the development of *Brama raii* and are therefore of doubtful phylogenetic significance here. The fin membrane connecting the posterior dorsal and anal fin rays extends beyond the scaly sheath to the tips of the fin rays in the 357 mm. fish, while in the 618 mm. one this membrane is limited to the proximal two-thirds of the fin; it does not extend beyond the scaly sheath.

In all other details, such as the distinctive shape of the caudal fin, the presence and nature of the transverse caudal grooves which lie immediately in advance of the dorsal and ventral procurent caudal rays, the dentition, the gill rakers and their minute accessory spines and tubercles and the general body form (exclusive of fins), the 357 mm. Gulf of Mexico individual is the same as that from Nova Scotia.

The differences between the 74 mm. juvenile (Pl. I, Fig. 2) and the 357 mm. adult are more striking. In pattern and number of scales, if not in the shape of the individual scale, the specimens are similar. The larger fish has 44 rows of scales between the upper margin of the gill opening and the base of the mid-caudal rays (where a sharp change in scale size occurs); the smaller one has 45. The number of longitudinal rows, from the mid-dorsal line in front of the origin of the dorsal fin to the mid-ventral line before the anal origin, is 27 in the larger fish and 26 in the smaller. The adult has 17 scales along the ventral mid-line between the origin of the ventrals and anus while the small fish has 15. Although the fin membranes are partially missing on the juvenile, traces of scale pockets similar to those of the adult can be found on the dorsal, anal and caudal fins. The distinctive axillary scales of both pectoral and ventral fins are alike in the two fish. The snout, branchiostegal membrane and rami of the lower jaw are equally scaleless in the two individuals.

The character of the individual scales, on the

other hand, differs greatly between these two fish. Each body scale of the 74 mm. individual bears a strong spine, a characteristic of all known juvenile bramids and pteraelids. Considering only the spines along the median row of scales, those anterior to the 34th scale are directed backward; the last ten are directed forward. In the 357 mm. fish only the antrorse spines on the posterior half of the body remain. All scales of Bigelow & Schroeder's 618 mm. fish are smooth. Each scale spine of the 74 and 357 mm. specimens originates near the center of the scale and protrudes through a notch in the posterior edge of the preceding scale. As the spines decrease in size anteriorly in the 357 mm. individual, these notches become less prominent. The same trend is apparent when a scale of the 74 mm. specimen is compared with one from the same point on the body of the 357 and 618 mm. specimens. Accompanying this change in scale form is a decrease in height of each scale. In the juvenile, the greatest height of a scale taken from the side of the body behind the pectoral fin is 3.5 to 4 times its greatest width, a ratio approaching the extremes encountered in such fishes as the grammicollepid zeoids and the bramid genus *Collybus*. The height of a scale from the same body location on the larger specimens is only one and one-half times its greatest width.

The premaxillary and mandibular teeth of the 357 and 74 mm. fish are very similar. The largest teeth of both jaws are the inner, anterior series of recurved canines. Some of the outer teeth of both jaws are directed slightly outward, a condition more apparent in the juvenile, in which the lips are somewhat macerated. The palatine teeth of the larger fish are better developed than those of the smaller. The vomer is toothless in both.

In number and shape of gill rakers and in position and degree of development of the accessory spines and hooks on each raker there are no significant differences between the 74 and 357 mm. fish. Exclusive of the rudiments, each has a raker count of 2+7. In addition, the epibranchial has three rudiments, which increase in length ventrally, and the hypobranchial has four. Each epibranchial raker has one or two medially-directed spines, while each raker of the ceratobranchial has three or four along its distal half. Each rudiment has a cluster of spines at its tip. In each fish there are also 4+9+4 spine-bearing tubercles on the inner side of the first gill arch. The 357 mm. specimen differs from the juvenile only in having 4 rather than 3 rudiments on the epibranchial, 6 instead of 4 on the hypobranchial, and in better developed spinules on the gill rakers and tubercles.

It is in the position and nature of the fins that the greatest differences between the juvenile and the adult are seen. Paramount among these is the nature of the dorsal and anal fins—falcate, with the rays filamentous and scarcely branched in the juvenile, less attenuated and with the rays branched in the larger fish (Table 1). The apparent difference in the position of the ventral fin could easily accompany growth from 74 to 357 mm., as could an increase in the amount of dermal material which supports the dorsal, anal and caudal lobes. A reduction in the length of filamentous fin rays is also undoubtedly a consequence of growth; such losses are known to occur during the development of many diverse species. Many fishes, conservative in form as adults, are adorned with various filamentous appendages as young. The change from lack of true branching in the fin rays of the juvenile cannot as readily be attributed to growth as these other fin differences, although juveniles of *Brama* have undivided or very weakly divided rays which later become fully branched (Lütken, 1880, pl. 4; Schmidt, 1918: 5).

No lateral line is visible on the 618 mm. specimen reported by Bigelow & Schroeder. The 357 mm. specimen, on the other hand, displays a series of about 13 modified scales which appear to represent a poorly-developed lateral line. This series begins above the upper end of the gill opening and arches posteriorly to a point below the middle of the dorsal lobe. A series of more typical lateral-line pores can be found on the corresponding scale row in the 74 mm. specimen. This series, also composed of 13 scales and terminating beneath the dorsal lobe, is slightly more arched than in the larger fish.

In both adult fish the premaxillary terminates anteriorly on a horizontal with the center of the eye and extends posteriorly to beneath the center of the eye. The free edge of the opercular bone is thin, entire and irregular in outline. The margins of the sub-, inter- and preopercle are membranous. There are slight differences in degree of ossification and in the shape of the orbit. In both fish the orbit is nearly circular, while in Bigelow & Schroeder's 618 mm. fish the orbit is vertically elongate (the horizontal axis is contained 1.3 times in the vertical).

Both specimens have prominent transverse caudal grooves which lie above and below the caudal peduncle anterior to the procurent caudal fin rays.

Although a direct comparison of the three additional Gulf of Mexico fish with the 618 mm. *Taractes* from Nova Scotia was not possible, no significant differences were found between these and the 357 mm. fish discussed above. The counts and measurements of the six western

TABLE 1.—COUNTS AND MEASUREMENTS OF SIX SPECIMENS OF *Taractes longipinnis*
FROM THE WESTERN NORTH ATLANTIC

	Bigelow & Schroeder, 1929, Nova Scotia	Oregon Station 1173	Oregon Station 1173	Oregon Station 1112	Oregon Station 1317	Oregon Station 1043
Standard length (mm.)	618	376	371	357	349	74
Fork length (mm.)	670	418	413	394	390	85
Counts:						
Dorsal fin ¹	35	38½	37½	37½	37½	37
Anal fin ¹	28	29½	30½	29½	28½	28
Pectoral fin	20	22/22	21/21	21/20	21/21	20/21
Scales ²	43	46	45	44	47	43
Gill rakers ³	2+7	2+7	2+8	2+7	2+7	2+7
Measurements (% of standard length)						
Length of head	32.4	29.8	31.3	29.4	29.8	34.5
Length of snout	10.2	7.2	9.2	8.4	7.2	8.1
Length of premaxillary	14.7	14.4	15.1	14.6	13.8	16.9
Horizontal diameter of eye	6.6	5.9	6.5	5.9	6.3	10.8
Vertical diameter of eye	8.4	6.4	7.3	6.7	6.9	10.1
Width of interorbital	12.9	12.5	12.7	12.3	12.3	12.1
Greatest depth of body	52.1	54.5	55.0	55.5	55.3	58.8
Least depth of caudal peduncle	7.4	6.6	6.2	5.9	6.3	8.1
Snout to origin of anal fin	56.7 ⁴	53.7	55.2	58.8	56.1	54.0
Snout to origin of ventral fin	36.5 ⁴	32.5	34.2	37.5	33.8	30.4
Snout to origin of dorsal fin	44.8 ⁴	41.8	44.2	41.2	44.4	43.2
Height of dorsal lobe	28.3	49.5	51.7	47.9	50.7	63.5
Height of anal lobe	28.2	53.5	54.7	53.8	53.0	70.3
Length of mid-caudal rays	8.5	11.2	11.3	10.4	11.7	14.9
Length of pectoral fin	38.2	39.9	37.7	35.0	36.4	21.6
Length of ventral fin	7.0	8.5	6.7	8.4	8.3	12.1

¹A combined count is used here since it is impossible to distinguish accurately between spines and soft rays without removing the overlying skin and scales.

²The row of scales which extends from the upper end of the gill cleft to the base of the caudal fin, exclusive of the small scales which cover the caudal base.

³Exclusive of rudiments.

⁴From Bigelow & Schroeder's figure (1929, pl. 1).

North Atlantic specimens are recorded in Table 1.

I mention the shapes of the caudal fins of these four Gulf of Mexico adults since they may be of later taxonomic interest. Two nominal species of *Taractes*, *T. brevoorti* and *T. saussuri*, are characterized by their biconcave caudal fins, *i. e.* the central rays of that fin are longer than those flanking them. In one of the four adult *Taractes* from the Gulf the central rays equal in length those on either side; in two others they are very slightly shorter, and in the fourth they are slightly longer. In none, however, is the

margin of the caudal as strongly biconcave as in *T. brevoorti*.

In summary, the six western North Atlantic specimens of *Taractes* differ in the following respects: the shape of the caudal and ventral fins, form of the individual scales, presence or absence of poorly-developed lateral-line scales, shape of the eye, slight differences in body proportion, presence or absence of branching in dorsal and anal rays, and extent of the dorsal and anal fin membranes. Growth from juvenile to adult occurs in a less conservative manner in the *bramids* than in most *acanthopterygian*

fishes, in which an array of distinguishing features such as these would be of considerable taxonomic and nomenclatorial interest. In the Bramidae, however, differences between individuals of different size must be evaluated with reference to the great ontogenetic changes which are known to take place.

I do not hesitate to ascribe the decrease in relative height of the dorsal and anal lobes with increasing size to normal allometric adult growth (Pl. II, Fig. 3; Barnard, 1948: 374). Similarly, all known bramid juveniles have a spine on each scale which is gradually lost with growth; it is therefore appropriate to believe that the reduction in scale armature with increase in size in our series is a function of growth. I likewise ascribe the progressive shortening of the relative height of the individual scale to normal ontogenetic change, but feel hesitant about the significance of those scales in the 74 and 349-376 mm. fish which appear to represent a lateral line. Because of the intricate pattern and bizarre form of all scales it is difficult to trace the reduction in these possible lateral-line rudiments, if such a reduction occurs. Fitch (1953: 539) reported a lateral line in his 590 mm. California *Taractes*, and Jordan's *Eumegistus illustris*, obviously closely allied to, if not congeneric with, *Taractes*, has a lateral line. The lateral line may be variable in *Taractes* and will deserve close attention when a larger series becomes available.

If this evaluation is correct, the five western North Atlantic adult *Taractes* can be referred to a single species, for the only difference which distinguishes the four Gulf of Mexico fish from the larger one from Nova Scotia is the extent of the posterior dorsal and anal fin membranes. In the fish of 618 mm. the tips of the posterior dorsal and anal rays are free from the membrane; in the Gulf of Mexico fish the tips lie within this membrane. This characteristic is among those listed by Bigelow & Schroeder (1929: 45) as diagnostic of *Taractes princeps*. I hesitate to afford it such distinction, since the only *Taractes* which possess it are the largest known individuals: Bigelow & Schroeder's of 618 mm., Johnson's types of *T. princeps* (27 to 33 inches), Fitch's California fish (590 mm.) and, if it be admitted to *Taractes*, Jordan's *Eumegistus illustris* (about 608 mm.). In fishes such as some scombrids and carangids, the dorsal and anal finlets, separate and free from a connecting membrane in the large adult, are completely or partially enclosed in a fin membrane as juveniles and young adults. Parallel fin development may occur among the bramids.

An important difference between the 74 mm. Gulf juvenile and the five adults makes its identity with them less certain. In the juvenile *Tar-*

actes the posterior dorsal and anal rays are unbranched, although there is an indistinct line distally which separates the anterior half from the posterior. In the adults these rays are branched nearly from their bases. Since the rays of the juvenile bramids figured by Lütken (1880), Sanzo (1928) and others are similar to those of our juvenile although the adults have completely divided rays, the separation of species by this character can be questioned. However, because of this difference, the morphometric differences shown in Table 1, the great difference in size between this 74 mm. fish and the next-smallest known *Taractes* (300 mm. fork length—Barnard, 1948: 375, pl. 10), and the general confusion attending past work on the juveniles of most pelagic spiny-rayed fishes, this specimen was compared with other species closely related to it in appearance if not in phylogeny.

The scale pattern, fin structure, general physiognomy and especially the presence of distinct transverse caudal grooves distinguish our juvenile from all of the bramids other than *Taractes* to which I have compared it. *Brama raii* and *Collybus drachme* of about the same length as our fish (85 and 81 mm. in fork length respectively) are represented in the collections of Stanford University's Natural History Museum. These are totally different from the juvenile *Taractes*. Although the young of *Eumegistus illustris*, *T. brevoorti*, *T. raschi* and *T. saussuri* are unknown, none of the adults has the prominent transverse groove on the caudal peduncle, a groove which is well developed in our juvenile. The prolonged dorsal and anal fin rays, which are filamentous, with only the suggestion of branching, are reminiscent of those of the heterogeneous assemblage of species reported by Jordan (1919), but since the dorsal fin of our *Taractes* originates well behind the eye and the anal a considerable distance behind the ventral fins, I did not study in detail *Pteraclis* and the various nominal species of *Pterycombus* and *Centropholis* (Barnard, 1927: 598; Kuroshima, 1941: 56; Belloc, 1927: 239; and others). The juvenile *Taractes* is also quite distinct from the berycoid fishes which probably resemble it when young: *Trachyberyx barretoii* and *Trachichtodes spinosus*. There is little reason to believe that the 74 mm. Gulf juvenile belongs to a genus other than *Taractes*.

Taxonomic status of the western North Atlantic TARACTES.—Although most of the nomenclatorial and taxonomic difficulties which confronted Bigelow & Schroeder when they reviewed this genus in 1929 are still extant, more recent work and additional material justify a reappraisal of *Taractes* taxonomy here.

With the exclusion of *Collybus* Snyder and *Eumegistus* Jordan & Jordan, the Bramidae can be divided into the two natural groups proposed by Smitt (1892-95) and recognized by Bigelow & Schroeder (1929): those forms with more than 70 scales in a median series, *Brama*, and those with fewer than 60, *Taractes*. I am concerned here only with the few-scaled species, of which the following nominal representatives are known:

<i>Taractes asper</i> (Lowe, 1843)	Madeira
<i>T. longipinnis</i> (Lowe, 1843)	Madeira
<i>T. brevoorti</i> (Poey, 1861)	Cuba
<i>T. raschi</i> (Esmark, 1862)	Norway
<i>T. princeps</i> Johnson, 1863	Madeira
<i>T. saussuri</i> (Lunel, 1866)	Cuba
<i>T. steindachneri</i> (Döderlein, 1883)	Japan
<i>T. platycephalus</i> Matsubara, 1936	Japan
<i>T. miltonis</i> , Whitley, 1938	Australia

I have tentatively omitted *Eumegistus illustris* Jordan & Jordan (1922: 36) from *Taractes*, although its close resemblance cannot be ignored. Because of its lateral line and smooth-edged scales, *Eumegistus* has been considered generically distinct from *Taractes*, but I have noted above the variation in the lateral line found in specimens of *Taractes*, and both the scale spine and the notch in the rear edge of each scale in young *Brama* and *Taractes* disappear with age. Jordan & Jordan's type specimen of *E. illustris* was a large individual, about 608 mm. in length. There are, however, meristic differences between *E. illustris* and the nominal species of *Taractes*.

Fowler (1938: 44) based his description of *Brama leucotaenia* on a juvenile specimen 22.5 mm. in standard length from the Philippine Islands. Fowler compares his fish with *Brama raii* and distinguishes it from that species by the pigmentation of the dorsal fin. However, his comparison of *B. leucotaenia* with *B. raii* is of little moment since the large scales (53 in a median longitudinal series) show it to be more closely related to *Taractes*. Although I have examined Fowler's type (U.S. National Museum no. US 98817), I have not undertaken a detailed study of its relationship. Since in scale count, number of gill rakers (about 5+10) and position and extent of the lateral line it more nearly resembles *Eumegistus illustris* than any known *Taractes*, I consider this juvenile fish generically and probably specifically identical with *Eumegistus illustris*.

Collybus bears little resemblance to *Taractes* or *Brama*. More will be said of *Collybus* later.

The identity of *Taractes asper* is uncertain. Lowe's description is inadequate and the type (from Madeira) cannot be located. This fish has traditionally been considered a young stage of

T. longipinnis, which Lowe described on the preceding page of the same paper (1843: 82). However, *T. asper* may be the young of an entirely different bramid-like fish. Mr. G. E. Maul (in correspondence) has pointed out to me the similarity between Lowe's description of *T. asper* and the berycoid species *Trachyberyx barretoii* Roule. I can contribute no original information in clarification of this question and will omit *Taractes asper* from further consideration here.

Omitting *Eumegistus*, *Collybus* and *T. asper*, a natural subdivision of the remaining *Taractes* species suggests itself. Gross differences in body proportions and fin structure distinguish *Taractes longipinnis* of Lowe and its allies from the type of *T. raschi*, a second specimen referred to *T. longipinnis* by Smitt *et al.* (1892-95: 80), and Matsubara's *T. platycephalus*. In body form, fin structure and scale pattern, if not in more detailed features, there is little in common between these three fishes and representatives of the *T. longipinnis* group of similar size. The type figures of *T. raschi* and *T. platycephalus* are reproduced here (Pl. II, Fig. 4; Pl. III, Fig. 5). It is unfortunate that Matsubara did not consider in more detail the resemblance between his *T. platycephalus* and Esmark's type of *T. raschi* rather than accepting Smitt's synonymy, which places *T. raschi* in the synonymy of *T. longipinnis*, and basing his comparison on Bigelow & Schroeder's paper. I have seen neither species, but if the fin structure and shape are subject to growth changes as pronounced as those in *Brama* and *T. longipinnis*, and if the vomerine dentition is as variable in *Taractes* as Lunel found it to be in *Brama*, it is difficult to characterize *T. platycephalus*.

The second subdivision of *Taractes* includes the deeper-bodied species in which both young and adults have strongly falcate dorsal and anal lobes, more steeply inclined foreheads, and distinctive squamation: *T. longipinnis* (Lowe, not of Smitt), *T. princeps*, *T. brevoorti*, *T. steindachneri*, *T. saussuri* and *T. miltonis*.

Döderlein's *T. steindachneri* (in: Steindachner & Döderlein, 1883, pl. 7) has been referred to the synonymy of *T. longipinnis* by Steindachner & Döderlein (1884: 174), a disposition accepted by Bigelow & Schroeder. It was resurrected by Jordan, Tanaka & Snyder (1913: 134), Matsubara (1936) and others on the basis of slight differences in scale and fin-ray counts. The species might better have remained in synonymy.

Taractes brevoorti and *T. saussuri* (Pl. III, Fig. 6) are alike in having a double-concave caudal fin. Although one of the Gulf of Mexico adults which I have examined has central caudal rays slightly longer than those flanking them,

no recent specimens of *Taractes* approach the extreme condition shown by *T. saussuri*. These two species must be retained. *T. brevoorti* appears to be closely related to *T. longipinnis*. *T. saussuri*, on the other hand, is intermediate between *T. longipinnis* and *T. raschi* in body form and fin structure. Nothing further can be said about these species until specimens become available.

Whitley (1938: 193) distinguishes his Australian *Taractes miltonis* from the fish described by Bigelow & Schroeder (1929) as follows:

"Head, body, scale, and fin characters agreeing excellently with the detailed description of the allied *Taractes princeps* (Johnson) recently given by Bigelow and Schroeder (Bull. Mus. Comp. Zool. Harvard, lxi., 2, February, 1929, p. 45 and plate —) but is of slightly larger size and is distinguished by having the eye-diameter about one-fourth, instead of about one-fifth the length of the head; anal lobe considerably shorter than head; comparatively longer pectoral and ventral fins; distance from ventral origin to anal origin notably less than length of head; different gill-rakers, etc."

Whitley does not describe the differences in gill rakers. The horizontal diameter of the eye of his specimen is 7.2 percent. of standard length *cf.* 5.9-6.6 in the western North Atlantic adult specimens (Table 1); the vertical diameter is 8.3 *cf.* 6.4-8.4. The head length he reported, 200 mm. or 27.8 percent. of standard length, is 2 percent. shorter than any known western North Atlantic adult. I have noted elsewhere the relative reduction in the height of the anal fin lobe with increasing length of fish in *Taractes longipinnis* and Whitley's measurement, 140 mm. or 19.5 percent. of standard length, is not out of accord with this growth change. There is no notable difference in the distance between the origins of the ventral and anal fins between Whitley's fish and Bigelow & Schroeder's (about 1 percent. of standard length), and his measurements of the lengths of the pectoral and ventral fins (35.9 and 7.65 percent. respectively) are within the range of the adult western North Atlantic material (35.0-39.9 percent. and 6.7-8.5 percent. respectively). *Taractes miltonis*, as described by Whitley, is devoid of distinguishing characteristics. This species, along with *T. steindachneri* and *T. princeps*, should go into the synonymy of *T. longipinnis*.

Taractes longipinnis and *T. princeps* were subjected to a detailed comparison by Bigelow & Schroeder (1929). These authors tentatively retained both species, listing the following combination of characters as diagnostic of *T. princeps* (p. 45):

1. Very deeply lunate tail.
2. The fact that the low rays of the anal and

dorsal fins are distally free from the membrane for about a third of their length.

3. Great length of the anterior dorsal and anal rays.
4. Scales smooth, without hooks or spines (at least in adult).
5. Caudal pits present."

Bigelow & Schroeder's recognition of both species reflects a careful study of the problem and is the more conservative course. Since neither type is still extant, an understanding of the relationship between *Taractes longipinnis* and *T. princeps* awaits the comparison of series of specimens from the type locality, Madeira. Maul, however, who has seen many *Taractes* during his long association with the Madeiran fishery, can distinguish but one species, which he refers to *T. longipinnis* (personal communication). If it seems probable that a large series of specimens would show that the two nominal species are identical, it would be reasonable to combine the two at this time—the course recommended by those ichthyologists who have been able to examine more than one specimen. I prefer this alternative, for my material influences the interpretation of three of the distinguishing characteristics afforded *T. princeps* by Bigelow & Schroeder and the remaining two are of dubious significance in the absence of confirming material. If my 74 mm. juvenile and Barnard's 268 mm. adult are correctly referred to *Taractes*, the shape of the caudal fin changes with growth from a shallow fork to the deeply lunate form seen in the largest specimen. Similarly, there can be little doubt that the lobes of the dorsal and anal become relatively shorter during adult growth, and that there occurs a loss of scale spines and a change in the shape of the scale itself during development. Two peculiarities remain to characterize *T. princeps*: the presence of caudal pits and the absence of an interradial membrane between the posterior dorsal and anal rays. Lowe did not mention caudal grooves in his brief description of *T. longipinnis*. They may or may not have been present. As noted elsewhere, the dorsal and anal rays are free from the interradial membrane only in the largest *Taractes*, and this difference alone seems inadequate for the separation of *T. longipinnis* and *T. princeps*.

I have not attempted to review the generic nomenclature. I cannot concur in deBuen's (1935: 102) union of *Brama* and *Taractes* or with his suppression of the generic name *Brama* in favor of *Lepidotus*. *Lepidotus* Asso (1801) was used by deBuen (1935: 102), Whitley (1938: 191) and Fowler (1949: 74) in place of *Brama* (Bloch & Schneider, 1801: 98) — the needless suppression of a generic name which

had been universally accepted for more than a century. The respective dates of publication, within the year 1801, have not been determined or at least were not discussed by the recent proponents of the generic name *Lepidotus*. *Taractes* is used here because it has been applied customarily to the species discussed in this paper and because there is no nomenclatorial reason for its suppression.

Since I have concluded that all of the individuals which are known from the western North Atlantic are alike and that this series possesses features which weaken the argument provided by Bigelow & Schroeder for the separation of *T. princeps* and *T. longipinnis*, I suggest that the population represented by these individuals should bear the name *Taractes longipinnis* Lowe.

I propose the following tentative synopsis of the species of *Taractes*:

I. Fewer than 50 scales in a median longitudinal series exclusive of the small scales overlying the base of the central caudal fin rays.

A. Caudal fin "rounded." (A species of uncertain identity).....*T. asper*

AA. Caudal fin emarginate, forked or biconcave.

B. Standard length more than twice the greatest body depth. Pectoral fin with 17-18 rays.

C. Caudal fin emarginate. Forehead concave, less than an eye's diameter between upper edge of eye and dorsal profile of head.

D. Vomer toothed. (North Atlantic; syn.: *T. longipinnis* of Smitt, not of Lowe).*T. raschi*

DD. Vomer toothless. (Japan).

T. platycephalus

CC. Caudal fin biconcave; tips of central rays on a line with tips of the outer caudal rays. More than an eye's diameter between eye and dorsal profile. Forehead convex. (Cuba).*T. saussuri*

BB. Standard length less than twice the greatest body depth. Pectoral fin with 19-21 rays.

E. Caudal fin emarginate. (Atlantic and Pacific; syn.: *T. steindachneri*, *T. princeps*, *T. miltonis*, not *T. longipinnis* of Smitt).*T. longipinnis*

EE. Caudal fin biconcave. (Cuba).

T. brevoorti

IV. *Collybus drachme*

As well as from the type locality (Hawaii), *Collybus drachme* Snyder (1904: 525; fig. 7) has been caught off Bermuda (Kanazawa, 1952:

80). Twelve specimens have been taken in the Gulf of Mexico, all from the stomachs of yellowfin tuna and lancet fish (*Alepisaurus*) caught at the five Oregon stations listed earlier in this paper. They range in standard length from 33.0 to 52.5 mm. and are in various stages of digestion. A 42.5 mm. fish was cleared and stained and examined for skeletal characteristics. I have also compared the twelve specimens with Snyder's type and cotypes, which are now in the U.S. National Museum and in the Natural History Museum, Stanford University.

I use Snyder's trivial name, *drachme*, for these Gulf of Mexico specimens since I have found no significant differences between representatives from the two oceans.

The largest known *Collybus* which has been described or figured is Snyder's 81 mm. Hawaiian type. Fowler (1928: 138) reported three larger (167-186 mm.) specimens obtained in Honolulu and now in the Bishop Museum and Jordan & Jordan (1922: 35) referred to a cast of a large individual, also in the Bishop Museum. A photograph of this cast portrays a fish about 155 mm. in length, but few details of the original fish can be discerned. The physiognomy and shape and position of the fins are similar to those of *Brama* and to Snyder's larger specimens of *Collybus*. This cast was certainly not made from a *Taractes*. Some authors have suggested that *Collybus* represents the young of a species of *Brama* or *Taractes*, a view that I am reluctant to accept. The scale count separates *Collybus* from *Brama* (45-55 cf. 70-80 in *Brama*) and our juvenile *Taractes*, 74 mm. long, is much thicker-bodied and has more falcate fins than any *Collybus* that I have seen. *Collybus* may represent a young *T. raschi* or *Eumegistus*, but pending evidence to the contrary, *Collybus drachme* should be recognized.

The following diagnosis is a composite taken from my twelve Gulf individuals, no one of which is undamaged:

Body compressed, elliptical in outline with a ventral profile more strongly convex than the dorsal. Eye large and circular, not entering into the dorsal profile, eye diameter 2.5-2.7 in head. Mouth oblique, premaxillary extending to beneath middle of pupil. Lower jaw coterminous with upper or slightly protruding. Head 3.0-3.4 in standard length; opercular bones smooth, although the elongate scales overlying the free edges are serrated. Greatest depth of body, at origin of dorsal fin, 1.5-1.8 in standard length. Least depth of caudal peduncle 3.5-4.5 in head. Lateral line usually absent, occasionally present, complete or incomplete. Head and body lightly pigmented, a sprinkling of melanophores below

orbit, along bases of all fins, on peritoneum and along dorsal edge of body.

D.: 32-34. A.: 28-29. P.: 20-21. Gill rakers: 2-3 + 8-9. Scales in a median series: 46-54; about 18 horizontal rows on body, counted obliquely upward and backward from the origin of anal fin. Vertebrae (one specimen only): 38.

Snout and forehead in front of center of eye scaleless but covered with small pores. Remainder of head and body scaled. Scales along bases of dorsal and anal fins and in axil of pectoral and ventral fins. Scales varied, those on head more strongly ctenoid than those on body. All scales vertically elongated, those on middle of body extremely attenuated, the width contained about nine times in the height. All scales with a vertical ridge and a central protruding spine or knob. About 14 keeled scales along the ventral midline between origin of pelvic fins and that of anal.

Teeth on jaws; none on vomer or palatines. Mandibular teeth in a single row posteriorly, a band anteriorly. Outermost anterior teeth recurved and enlarged. Two fangs at inner edge of anterior band at tip of mandible. Premaxillary teeth similar to those on mandible, but without anterior fangs.

Measurements, expressed as percent. of standard length: length of head, 29.9-33.9; length of snout, 5.3-7.7; length of premaxillary, 14.7-16.9; diameter of eye, 11.4-12.7. Greatest depth of body, 56.8-66.2 (decreasing with increasing length of fish), least depth of caudal peduncle, 8.3-12.7. Height of dorsal lobe, 21.1-23.9; height of anal fin, 8.4-10.4; length of pectoral fin, 27.4-32.2; length of ventral fin, 10.6-12.3.

V. SUMMARY

Except for the controversial *Steinegeria rube-scens*, no species of non-pteraclid bramid fish has hitherto been reported from the Gulf of Mexico. The off-shore collections of the U.S. Fish and Wildlife Service vessel *Oregon* contain representatives of two such species, which are identified here with *Taractes longipinnis* Lowe and *Collybus drachme* Snyder. Both are described, growth changes in *Taractes longipinnis* are discussed, and the nominal species of *Taractes* are reviewed.

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EXPLANATION OF THE PLATES

PLATE I

FIG. 1. *Taractes longipinnis* from Oregon station 1112 (Gulf of Mexico). Standard length: 357 mm. (Photograph courtesy of the Woods Hole Oceanographic Institution).

FIG. 2. *Taractes longipinnis* from Oregon station 1043 (Gulf of Mexico). Drawn, with some reconstruction, from a damaged juvenile 74 mm. in standard length. (Drawn by Janet Roemhild).

PLATE II

FIG. 3. Profiles of five specimens of Atlantic *Taractes longipinnis*. From the smallest to the largest, the data from which these profiles were drawn were taken from (a) the 74 mm. Gulf of Mexico juvenile; (b) a South

African adult of about 268 mm., from Barnard, 1948; (c) a 357 mm. Gulf of Mexico adult; (d) a 618 mm. adult from Nova Scotia, from Bigelow & Schroeder, 1929; and (e) a South African adult of about 706 mm., from Barnard, 1948.

FIG. 4. *Taractes raschi*. After Smitt *et. al.*, 1892-95, p. 80, fig. 24; from Esmark, 1862, pl. 1.

PLATE III

FIG. 5. *Taractes platycephalus*. From Matsubara, 1936, p. 297, fig. 1.

FIG. 6. *Taractes saussuri*. From Lunel, 1866, pl. 2.

FIG. 7 *Collybus drachme* from Oregon station 1065 (Gulf of Mexico). Standard length: 33.0 mm. (Drawn by Janet Roemhild).

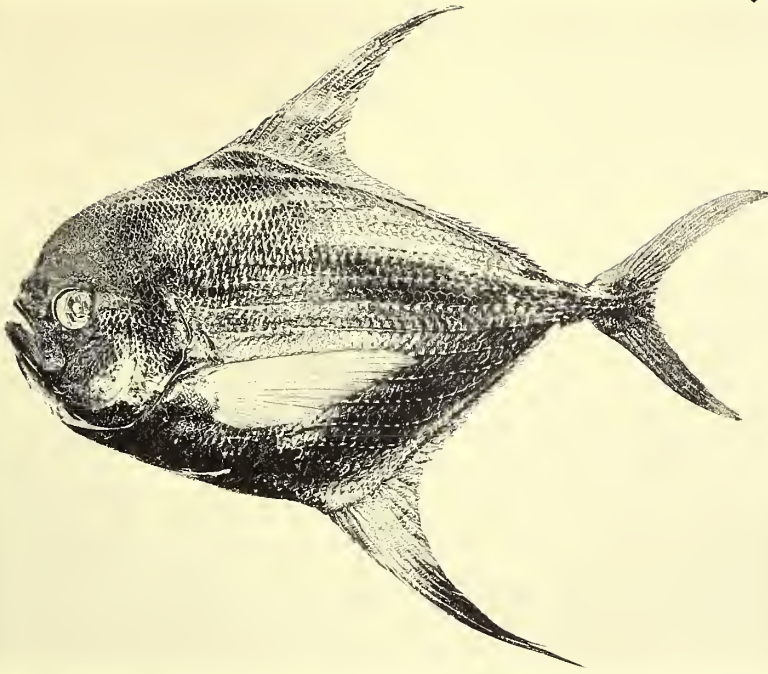


FIG. 1

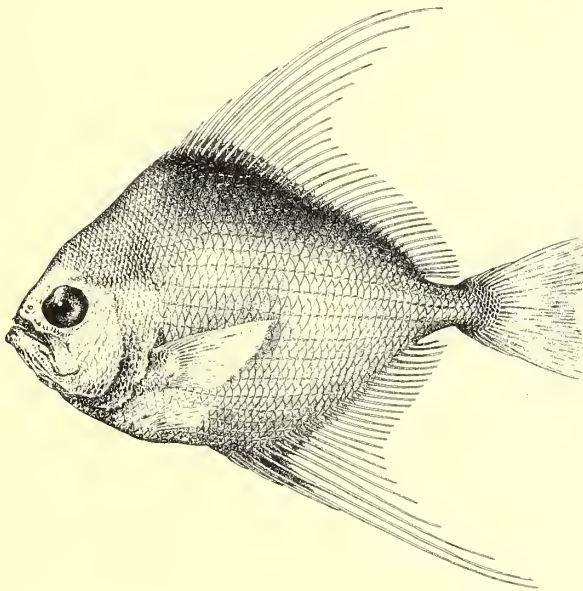


FIG. 2

ON THE BRAMID FISHES OF THE GULF OF MEXICO

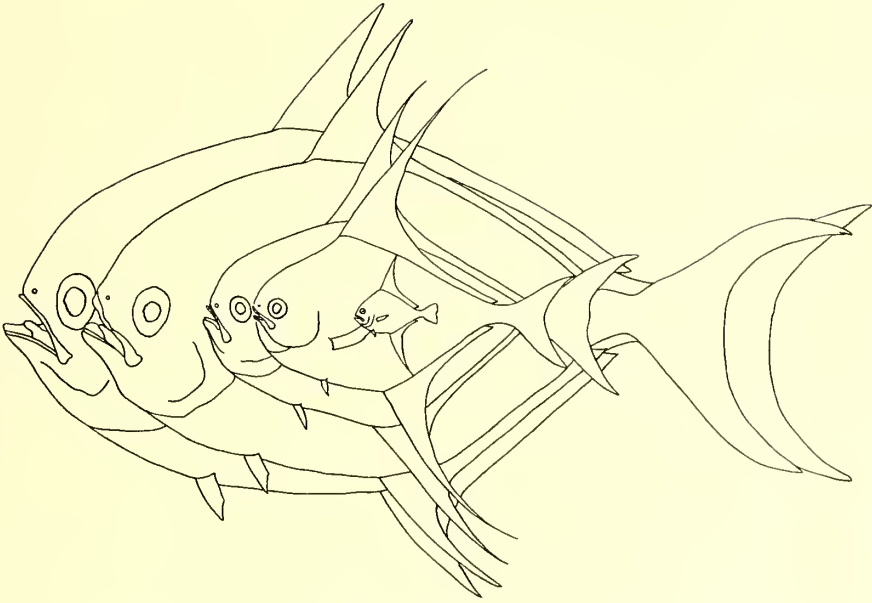


FIG. 3

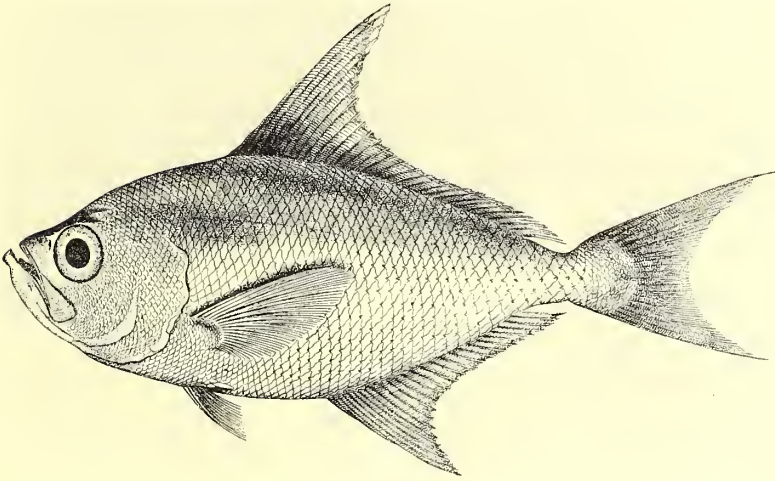


FIG. 4

ON THE BRAMID FISHES OF THE GULF OF MEXICO

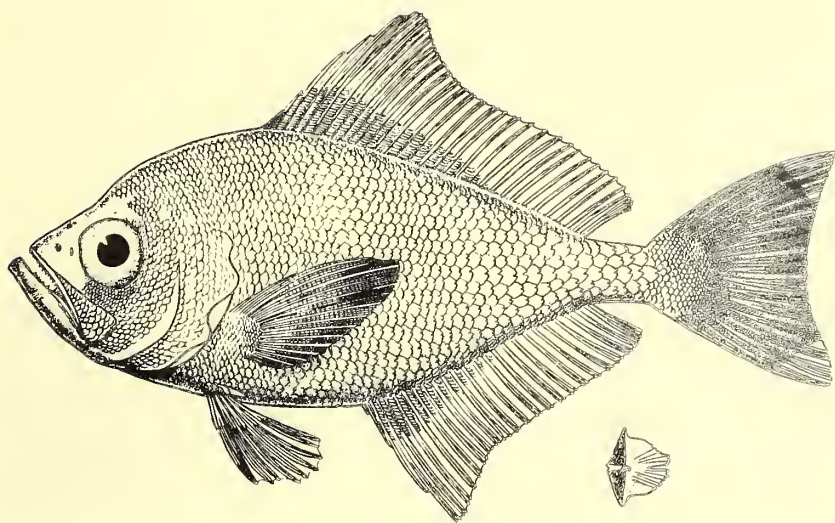


FIG. 5

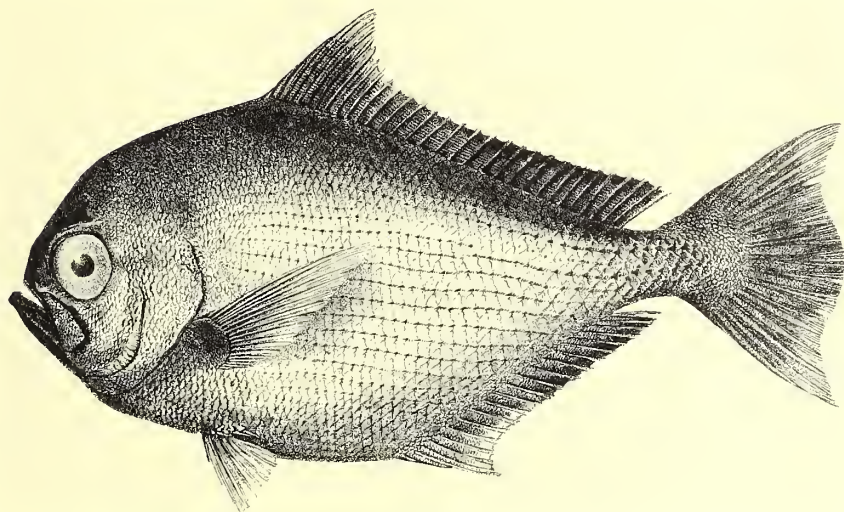


FIG. 6

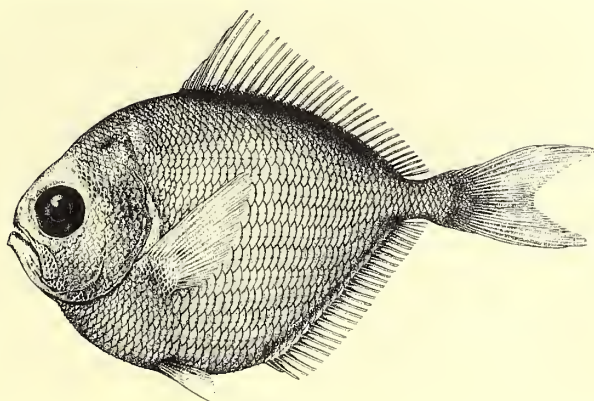


FIG. 7

The Relation of Oxygen Consumption to Temperature in Some Tropical, Temperate and Boreal Anuran Amphibians¹

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(Text-figures 1 & 2)

PREVIOUS studies on the geographic variation in climatic adaptation for poikilotherms have revealed much of physiological, ecological and evolutionary importance. The literature in this field has been thoroughly reviewed by Prosser (1955) and Bullock (1955). In respect to amphibians, investigations on the geographic variation of developmental adaptation in anurans (e.g. Moore, 1949; Volpe, 1954) have been particularly significant. Relatively little data, however, are available in which metabolic rate and temperature have been compared in amphibians from different latitudes. It is the purpose of this study, therefore, to present an analysis of the respiratory metabolism of some tropical, temperate and boreal anurans when compared at two similar temperature levels.

The tests were carried out on five species of tropical frogs: *Hyla maxima* and *Hyla crepitans* (Hylidae); *Leptodactylus typhoni* and *Eupemphix pustulosus* (Leptodactylidae) and *Prostherapis trinitatis* (Dendrobatidae). The temperate and boreal forms included the toads *Bufo boreas boreas* and *Bufo boreas halophilus* (Bufonidae); and the frogs *Rana clamitans* and *Rana sylvatica* (Ranidae) and *Hyla crucifer*.

The experimental work was undertaken at Simla, field station of the Department of Tropical Research, New York Zoological Society, Arima Valley, Trinidad, B.W.I., and the Department of Zoology, Columbia University, New York, from December, 1954, to July, 1955.

We wish to thank Ernest Karlstrom of the University of California for sending us the *Bufo boreas* material from California. The assistance of Rosemary Kenedy during the work at Simla is also gratefully acknowledged. The respirometers were kindly loaned to us by F. John Vernberg of Duke University.

MATERIALS AND METHODS

All tropical frogs were collected in the immediate vicinity of Simla in the northern range of Trinidad at an elevation of around 800 ft. between December 26 and March 30. *Hyla crucifer* was collected near New York City in late April and early May, and *Rana clamitans* and *Rana sylvatica* from Bondville, Vermont (1,500 ft.), on July 3 and 4. Breeding individuals of *Bufo boreas boreas* were taken seven miles northwest of Juneau, Alaska (sea level), between June 1 and 10, and post-breeding forms of *Bufo boreas halophilus* from California at the following localities: Richmond, Contra Costa Co. (sea level); Russian River area, Sonoma Co. (sea level to 1,000 ft.) and Sequoia National Park, Tulare Co. (7,500 ft.) between June 1 and 19. The five tropical species ranged in weight from 0.5 to 45.5 gms., and the four temperate and boreal species from 0.84 to 56.1 gms.

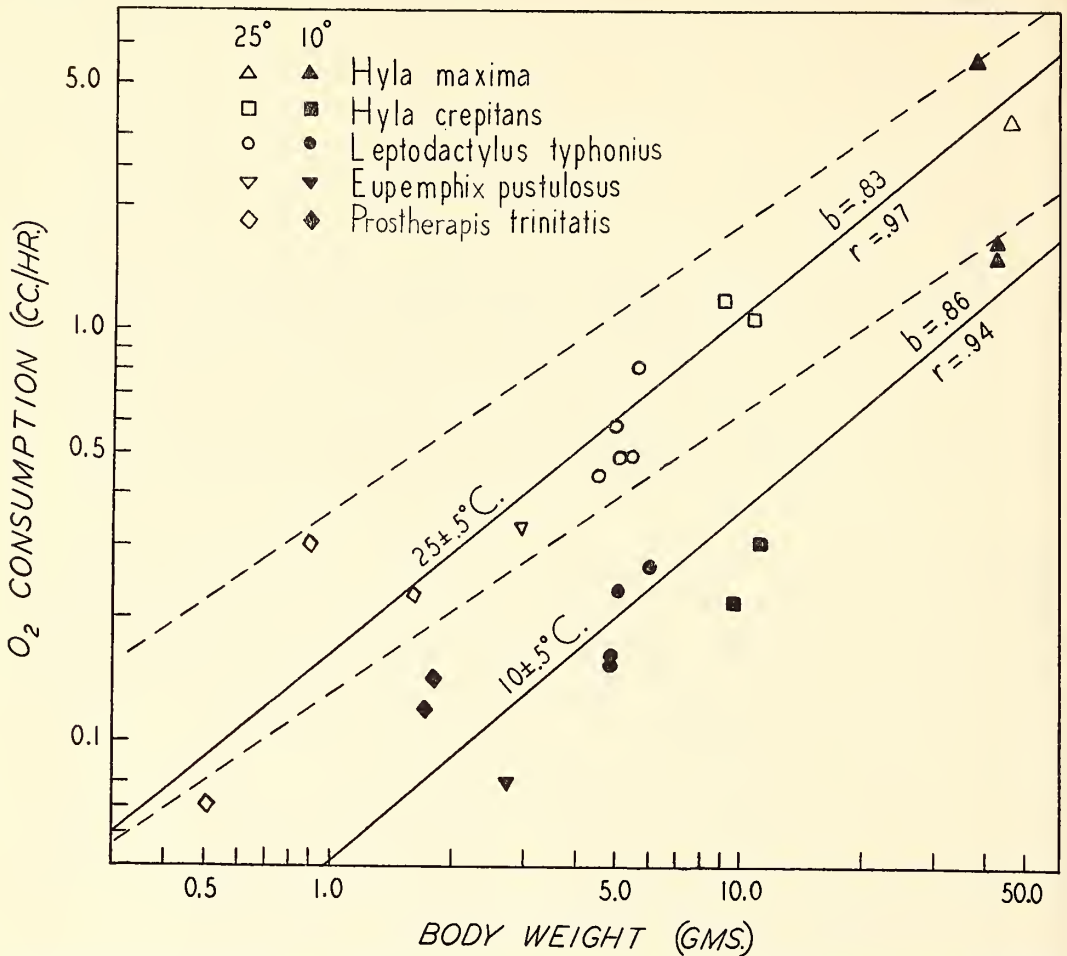
After collecting, the tropical frogs were maintained in aquaria at room temperature (20-25° C.), and the temperate and boreal forms were kept in aquaria in a constant temperature (15° C.) room. All were fed regularly on adult or larval insects.

Closed system volumetric respirometers of the type developed by Flemister & Flemister (1951) were employed for the determination of the respiration rates. Tests were conducted in water baths maintained at $25 \pm .5^\circ \text{C.}$ and $10 \pm .5^\circ \text{C.}$

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³This study was aided in part by the Arctic Institute of North America through funds granted by the Office of Naval Research.



TEXT-FIG. 1. The relation of oxygen consumption to weight in five species of tropical anurans at two temperature levels (b = regression coefficient; r = coefficient of correlation). Dashed lines represent regression slopes for temperate species.

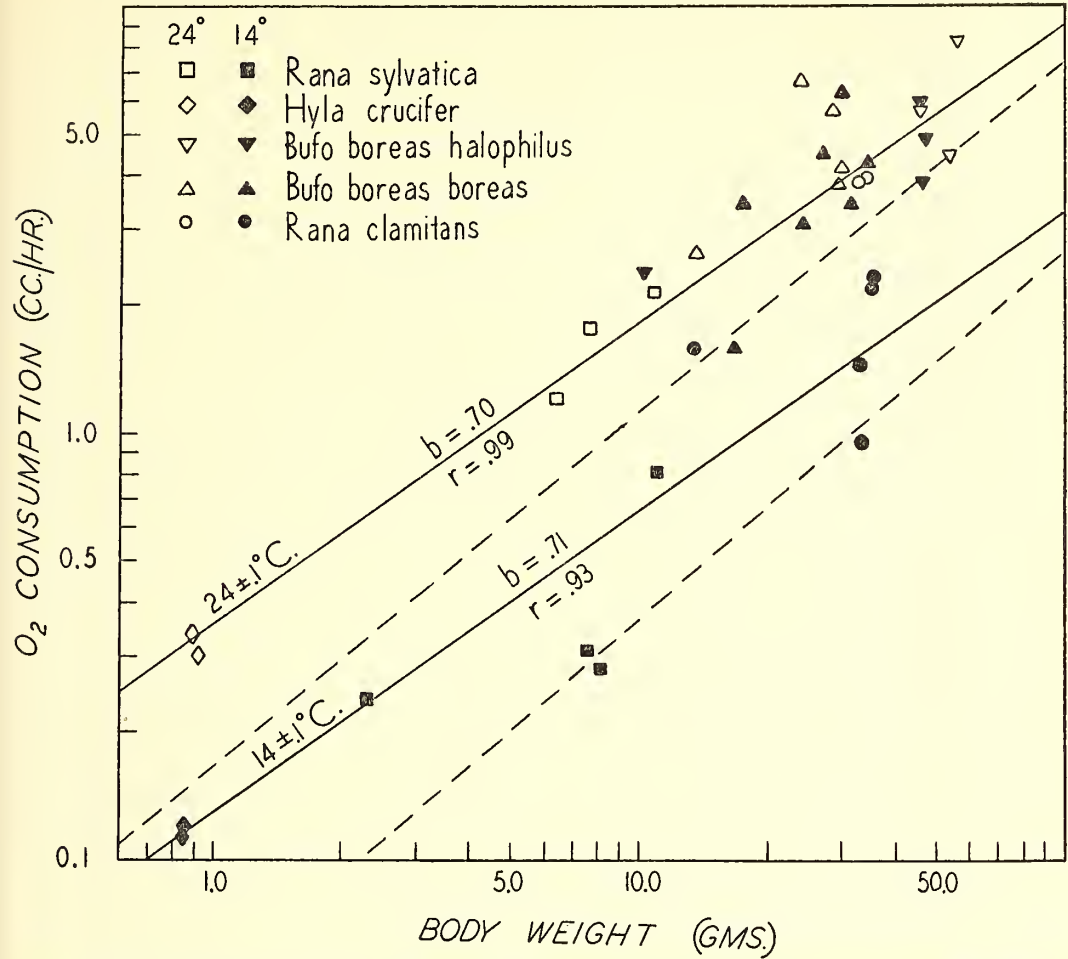
for the tropical forms and $24 \pm .1^\circ \text{C.}$ and $14 \pm .1^\circ \text{C.}$ for the temperate and boreal animals. After allowing a half hour for thermal equilibrium the tests were then run for a period of three or four hours. The volumes obtained for oxygen consumption have been corrected to standard temperature.

RESULTS

Text-figures 1 and 2 represent the double-logarithmic regression plots of weights to metabolism where the log of the rate of oxygen consumption (cc./hr.) equals $\log a + b \log W$, or metabolic rate equals aW^b , the constants a and b being the regression coefficients of the intercept and slope and W the wet body weights (gms.). Because of the slight depression for the values at 14°C. the data for *Bufo boreas*, although plotted, were not included in computing the regression lines for Text-figure 2.

At both temperature levels the respiratory rates for the tropical frogs averaged lower than those from the northern latitudes at similar temperatures. This appears to be especially evident when we compare the smaller animals, and is reflected in a steepening of the slope for the tropical weight regression coefficients. Although the average regression coefficient of .71 for the temperate animals at the two testing temperatures is but slightly higher than an exponent of $\frac{2}{3}$ (.67) that we might expect in keeping with the surface law of metabolism (metabolism/time = $aW^{2/3}$), the average slope of .84 for the tropical species seems significantly greater. There appears to be little correlation between temperature and regression slope in animals from the same general latitude.

With the exception of *Bufo boreas*, the temperature coefficients (Q_{10}) did not vary significantly between the tropical and temperate



TEXT-FIG. 2. The relation of oxygen consumption to weight in four species of temperate and boreal anurans at two temperature levels (b = regression coefficient; r = coefficient of correlation). Dashed lines represent regression slopes for tropical species. Data for *B. boreas* were not used in plotting the regression lines.

species (Table 1). The oxygen consumption rates for *Bufo boreas* at both temperature levels showed little variation both within and between the Alaskan and Californian forms. In fact, at both 14° and 24° C. the two races of *Bufo boreas* showed a metabolic rate typical of the temperate frogs tested at 24° C. This relative insensitivity to temperature change is reflected in their low temperature coefficients.

DISCUSSION

The weight regression coefficients (.703 and .707) for the temperate animals studied here are supported by the findings of others. Davison (1955) found a value of approximately $\frac{2}{3}$ (.67) for the exponent in seven species of temperate anurans (weight range 1 to 350 gms.) that he measured at 25° C., and Rubner (1924) reports an exponent of .67 for *Rana esculenta*. Regression coefficients of .80 and .85 are given by

Scholander *et al.* (1953) in the tropical and arctic animals (fishes, crustaceans, insects and spiders) that they measured at 0° C. (arctic species) and 20-30° C. (tropical species). No shift in the weight regression slope is apparent between the arctic and tropical forms. Because of the limited number of species tested by us in the present study, the steeper regression slopes (.825 and .861) found in the tropical species can not be considered as conclusive.

The compensatory metabolic rates exhibited by the northern or cold-adapted anurans studied here are in keeping with the general concept (Bullock, 1955) that activity rates are greater at a given temperature in cold-blooded animals from northern latitudes when compared with the same or closely related southern forms. Scholander *et al.* (1953) state that climatic adaptation in terrestrial poikilotherms is not

TABLE 1. SUMMARY OF DATA ON RESPIRATORY METABOLISM FOR ADULT TROPICAL, TEMPERATE AND BOREAL ANURANS AT TWO TEMPERATURE LEVELS.

Tropical Species	Sample Size	Weight (gms.)		QO ₂ (cc./gm./hr.)		Weight (gms.)		QO ₂ (cc./gm./hr.)		Q ₁₀
		Range	Mean	Range	Mean	Range	Mean	Range	Mean	
		10 ± 0.5° C.				25 ± 0.5° C.				
<i>Hyla maxima</i>	4	41.9-42.1	42.0	.035-.039	.037	37.4-45.5	41.4	.070-.121	.095	1.88
<i>Hyla crepitans</i>	4	9.6-11.1	10.3	.022-.026	.024	9.1-10.7	9.9	.101-.132	.116	2.87
<i>Leptodactylus typhoniuis</i>	9	4.8-6.0	5.1	.032-.046	.038	4.5-5.6	5.1	.098-.147	.115	2.10
<i>Eupemphix pustulosus</i>	2		2.7		.028		2.9		.117	2.61
<i>Prostherapis trinitatis</i>	5		1.7	.039-.071	.055	0.5-1.6	1.0	.139-.324	.201	2.38
Temperate and boreal species		14 ± 0.1° C.				24 ± 0.1° C.				
<i>Rana clamitans</i>	6	33.1-35.4	34.2	.028-.073	.051	33.0-34.4	33.2		.117	2.29
<i>Rana sylvatica</i>	6	7.5-11.0	8.8	.059-.075	.067	6.4-10.7	8.2	.186-.233	.206	3.07
<i>Hyla crucifer</i>	4		0.85	.097-.148	.122	0.89-0.91	0.9	.333-.382	.357	2.93
<i>Bufo boreas halophilus</i>	6	46.0-47.1	46.4	.084-.141	.107	45.6-56.1	51.7	.083-.147	.119	1.11
<i>Bufo boreas boreas</i>	9	24.2-34.8	29.5	.111-.210	.152	24.8-30.0	28.1	.131-.268	.181	1.19

significantly reflected by over-all oxygen consumption in the tropical and arctic insects and spiders that they tested at 0° and 20° C. Prosser (1955) also concludes that metabolic differences in populations are to be found in aquatic but not in terrestrial poikilotherms. If we consider the amphibians studied here as semi-terrestrial, we should then expect to find a significant, but not pronounced, difference in climatic adaptation between the tropical and northern forms. This appears to be the case. It would seem that a similar study of tropical and temperate reptiles would be of particular interest in this respect.

It is also generally accepted (Bullock, 1955) that cold-adapted poikilotherms tend to show a lower Q_{10} when compared with the same or closely related warm-adapted species. This concept becomes apparent among the anurans of this study only in the toad *Bufo boreas*. The other frogs show no significant variation in Q_{10} between tropical and temperate forms (Table 1). This seemingly inherent low Q_{10} for *Bufo boreas* could have been a contributing factor in its successful northern extension into southern Alaska. It is interesting to note, however, that in *Rana sylvatica*, which ranges even further north than *Bufo boreas*, we find no inherently lower temperature coefficient. These results can probably be partially explained by the limited number of determinations made as well as by the fact that we are here grossly comparing different species. Moreover, familial differences such as the more terrestrial habits of *Bufo boreas* could conceivably explain the dissimilarities. Breeding condition, size and seasonal fluctuations may also have had an influence. However, with the exception of *Hyla crucifer*, all northern animals were collected between June 1 and July 4, and only adults of similar weight within a species were used in the determination of the temperature coefficients. *Bufo boreas boreas* was the only form in breeding condition at the time of collecting. It is surprising that individuals of *Bufo boreas* exhibited such a persistently similar metabolic picture, coming as they did from two places so widely separated in latitude and altitude (sea level to 7,500 ft.).

There is good evidence in support of the conclusion (for references see Dehnél, 1955) that at their normal environmental temperatures, activity rates of closely related northern and southern animals are usually similar. The annual range of mean monthly temperatures for Juneau vary from -1.6° C to 13.0° C (1921-1950) with an annual mean of about 5.8° C. compared with a range of 25.6° to 27.3° C. and an annual mean of 26.5° C. for Trinidad (Port-of-Spain). If we

take the mean monthly temperature for June at Juneau (12.0° C.) and the average January to March monthly temperature for Simla (ca. 24° C.), we can then use the lower testing temperature (14° C.) for *Bufo boreas boreas* and the upper testing temperature (25° C.) for the tropical species as being reasonably close to their normal mean habitat temperature at the time of collecting. In examining the two extreme latitudinal forms of similar size (Table 1), we find *Bufo boreas boreas* with a mean oxygen coefficient (QO_2) of .152 at 14° C., which is higher than that of all but one of the tropical frogs tested at 25° C. At their normal habitat temperatures, then, the northern species showed the more active metabolism. Other studies (Scholander *et al.*, 1953, and Tashian, 1956) showed a higher QO_2 for the tropical forms at their normal environmental temperatures.

SUMMARY

1. The oxygen consumption of five species of tropical frogs from Trinidad, B.W.I., was determined and compared with that of four species of temperate and boreal anurans from Vermont, New York, California and Alaska at two temperature levels.

2. The respiratory metabolism for the northern forms averaged higher than that of the tropical animals at both temperatures. This higher metabolism for the cold-adapted animals is more evident in the smaller species, and is reflected in a steepening of the weight regression slope for the tropical species at both temperature levels.

3. With the exception of a lower Q_{10} for both races of *Bufo boreas* when compared with any of the other forms tested, no significant variation could be detected in the Q_{10} of northern and southern forms.

4. At their normal habitat temperatures, the northern species had a higher rate of respiration than the tropical species.

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Basic Patterns of Display in Fiddler Crabs (Ocypodidae, Genus *Uca*)^{1,2}

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(Plate I; Text-figures 1-4)

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I. INTRODUCTION

THIS contribution is a preliminary result of a general study of ocypodid crabs. The elaborate and varied displays characteristic of the fiddler crabs (genus *Uca*) appear to contribute substantially to an understanding of the phylogeny of the group. An interim report is presented because the increasing use of fiddler crabs in biological research makes their relationships of timely interest.

Specific differences in display behavior were described in an earlier study (Crane, 1941) where it was found that in a group of sympatric species of *Uca* on the west coast of Central America every species could be distinguished from every other species by the form of the display. Even species which could not be otherwise distinguished without a lens were easily identified at a distance by the characteristic form and tempo of the "waving" of the large cheliped. It

was found further that closely related species had similar types of display which were divisible into a number of groups.

During subsequent years other American species of *Uca* have been studied in the field on both sides of the continent, from California to Guayaquil, Ecuador, and from Massachusetts to Rio de Janeiro, Brazil (Crane, 1943, 1944 and unpublished).

Now, through a grant from the National Science Foundation, the work has been expanded into a world-wide program. In 1955 and 1956 the crabs were studied in Pakistan, Ceylon, Malaya, Singapore, Sarawak, the Philippines, north and northeast Australia, Fiji, Samoa, Tahiti and adjacent islands. Early in 1957 Panama was revisited, and previously known species reviewed in the light of the recent studies of Indo-Pacific forms. The behavior of the crabs, particularly of displaying individuals, was recorded in color on more than 9,000 feet of 16 mm. motion picture film. This material, along with the correlated and supplementary field notes, forms a permanent record for comparative laboratory analysis. The displays of about 19 good Indo-Pacific species of *Uca* have been recorded in this manner and 29 American forms. Although extensive field work remains to be done, particularly in Africa, the principal outlines of the development of display in the group appear now to be clear.

All detailed supporting data, discussion on the functions and releasing mechanisms of display, specific correlation of display with morphology and discussion of display in relation to infra-specific categories and speciation are reserved for a monographic report on the genus, now in preparation. The following subjects more or less closely associated with display will also be treated only in the later publication: color change, sound

¹ This study has been supported by a grant from the National Science Foundation.

² Contribution No. 975, Department of Tropical Research, New York Zoological Society.

production, territoriality, physical combat between males and the erection of structures near the burrows.

Among the many people who have facilitated the field work I wish at this time to express my appreciation particularly to Dr. William Beebe, Director Emeritus of the Department of Tropical Research, New York Zoological Society, and to Dr. Waldo L. Schmitt, Chief Curator of Zoology at the United States National Museum. Both were instrumental in inaugurating the study and, through the years, have given most helpful advice and encouragement.

II. GENERAL FORM OF DISPLAY IN FIDDLER CRABS

The outstanding characteristic of displaying fiddler crabs is a rhythmic elevation and lowering of the hypertrophied major cheliped of the male. In the few species usually familiar to western observers in the field this takes the form of "waving" or "beckoning," and is characteristic of the breeding season. The significance of the gesture has been described by various workers as non-sexually territorial, sexually territorial, a sex attractant, a challenge to other males and as various combinations of all of these possibilities. Although it is not proposed at this time to contribute further to the discussion, it may be said that field observations and motion picture records prove conclusively two points. First, all the suggested functions occur, sometimes all in a single species. Furthermore, in some advanced species there are distinct differences separating territorial, male-to-male and male-to-female displays, the latter being the most highly developed.

The motion of the cheliped is by no means always wavelike; in some species it is the merest slight raising of the flexed manus and chelae in front of the buccal region. In others it is a violent, very rapid shaking of the same parts at the level of the eye-stalks; in others the base of the manus is rapped against the ground, the waving is in jerks, or the cheliped is held high and revolved in circles. Among these extremes there are all degrees. Tempo is exceedingly various and specific, although unrelated crabs often wave at about the same rate of speed. Single waves range from one wave lasting 13 seconds to five waves being crowded into a single second. The first extreme of timing is found in certain South American populations of *U. pugnax rapax* under certain conditions and the second in an apparently undescribed species from Port Darwin, Australia. The waving rate of most species falls between one-half and two seconds per wave.

Motions associated with waving include elevation of the carapace on the ambulatories, re-

volving, moving from side to side, and various "bounces" and "curtsies" accomplished by rapidly lowering and raising the body on one or both sides.

In the following pages the display motion of the large cheliped will for convenience be termed "wave," whether or not it bears an anthropomorphic resemblance to such a gesture.

III. BASIC WAVE PATTERNS

Most of the species of *Uca* may be clearly divided into two groups depending on a basic difference in the direction of the first part of the motion of the major cheliped. These two behavioral complexes are characteristic of the majority of species in, respectively, the "narrow-fronted" and "broad-fronted" groups, as they have been termed in most systematic treatments.³

³ Bott, 1954, basing his decision on a collection of specialized Central American species of *Uca*, gave the narrow-fronted and broad-fronted groups each generic standing, reserving *Uca* for the narrow-fronts and proposing *Minuca* for the broad-fronts. Peters (1955), working on ecological and behavioral aspects of the same material, reduced *Minuca* to subgeneric rank. The present writer currently feels that *Minuca* should be given at most subgeneric status. This view is dependent on the extensive series of intermediate species distributed in other parts of the world, and on the distinctness and homogeneity of *Uca, sensu lata*, in comparison with all other genera in the family. Until further comparative morphological work is completed, it seems preferable to use simply the non-technical terms, "narrow-fronts" and "broad-fronts," as a practical division which for the majority of species appears to be phylogenetically justified.

Vertical Waves. (Text-figs. 1; 4, A-B). In the great majority of narrow-fronts, the cheliped at the beginning of the wave remains flexed in front of the buccal region and is raised up and slightly forward from there, without unflexing, until it reaches the level of the eyeballs. In the simplest displays it reaches no farther and therefore is never unflexed. In more advanced displays its elevation continues obliquely above the eyes, through the unflexing of the manus and chelae. Regardless of the amount of elevation or degree of unflexing, the cheliped is lowered back into rest position in the same plane in which it was elevated. This type of display will be called a "vertical wave."

Lateral Waves. (Text-figs. 3; 4, D-F). By contrast, the characteristic wave form of almost all species of broad-fronted *Uca* commences with a sweep to the side, rather than with a vertical elevation of the cheliped; this kind of gesture will be called a "lateral wave." In moderately intensive display, in which differences among species are most apparent, the flexed cheliped is pushed away from the body at the beginning

of the wave and more or less unflexed toward the side; it then sweeps up to a completely unflexed, high-reaching position. Finally it is flexed once more in front of the buccal region. Since it is often lowered in a direct path, close to the body, a more or less circular motion is completed. The amount of deviation from the path of the first part of the wave differs among species, and within species depending on the degree of display intensity; therefore the circularity varies widely; sometimes, in fact, lateral displays are altogether single plane. In displays of the lowest intensity of all, even laterality is often absent, the cheliped motion closely resembling the slight, flexed, single-plane display of the vertically waving narrow-fronts, as described in the preceding paragraph (Text-fig. 4 C).

Intermediate Waves. The waving pattern of a few species is intermediate between vertical and lateral types. Morphologically these forms also show some characters intermediate between those of narrow-fronts and broad-fronts.

Position of Body during Waving. In addition to the form of the wave there are several fundamental differences in the position of the body during waving. In some species it is scarcely raised at all; in many it is raised on the ambulatories and lowered with every wave; in still others it is raised and held erect during a series of waves. The amount of elevation varies somewhat within species in accordance with the intensity of waving.

Systematic Distribution of Basic Wave Patterns. An arrangement of species characterized by various types of wave is presented in Table 2. Authorities for the species, geographical distributions and localities where display has been observed are listed in Table I.

As will be seen from Table 2, the vertical type of wave is typical of Indo-Pacific narrow-fronts. These species in turn include those forms in which *Uca* display is simplest and, it seems unquestionably, most primitive. These uncomplicated displays are found in *manii*, *rhizophorae* (Text-fig. 1, A-B), *rosea*, *ischnodactyla* and *rathbunae*; in these species the body is scarcely if at all raised above the ground during display. *U. dussumieri* is somewhat further advanced. Although specific differences in the waving pattern of all of these are clear-cut, the group similarity is obvious to the observer. In all of these species the cheliped is not raised high overhead, and the amount of time devoted to waving is negligible in comparison with that so spent in the more advanced species.

The waving of still other narrow-fronts from the Indo-Pacific is considerably more advanced, as in *marionis*, *signata* (Text-fig. 1, C-D) and *zamboangana* (Text-fig. 1, E-F). Although the

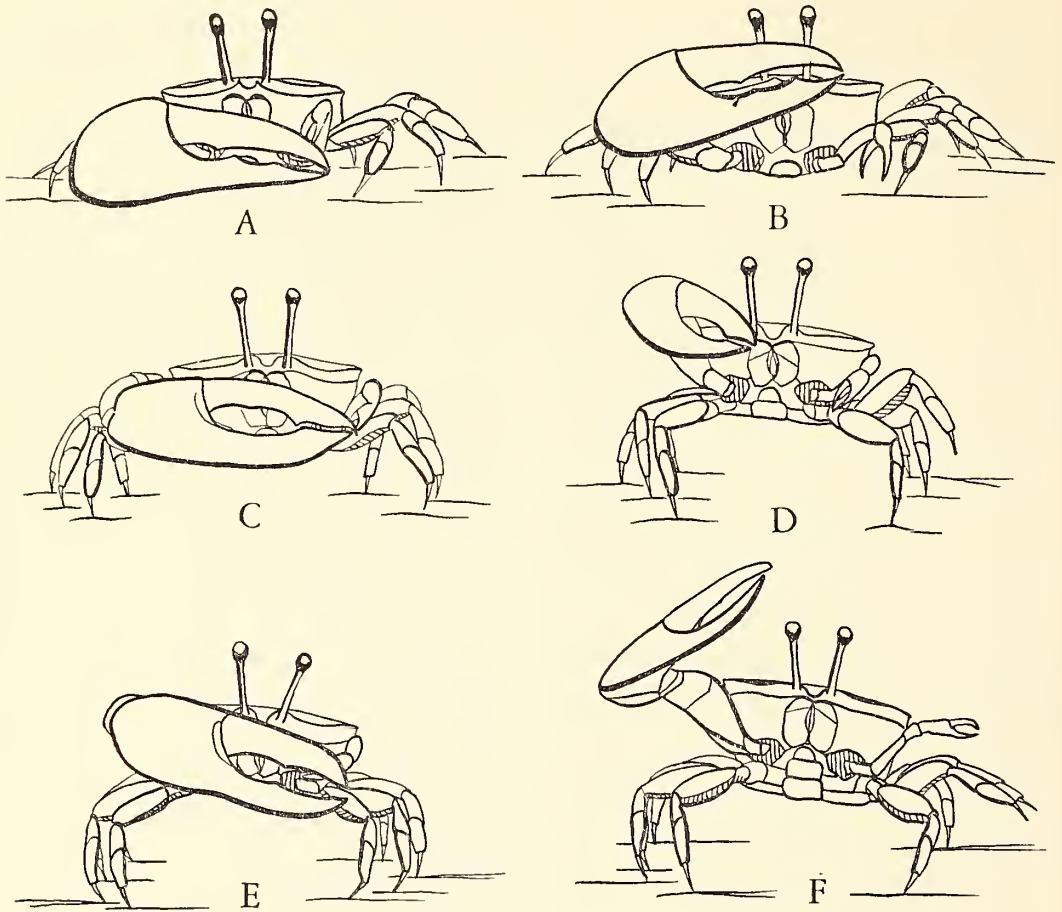
pattern is still vertical and single plane rather than lateral in character, the reach is higher, the tempo tends to be swifter, the proportion of time devoted to waving greater and the elevation of the body conspicuous.

Neotropical members of the narrow-fronted group are aberrant as well as intermediate, both morphologically and behavioristically. The display is characterized by a lateral, not vertical, type of wave. Except in low intensity display the gesture is spiral, rather than merely circular, since the cheliped, after its initial lateral elevation, is revolved throughout a series of waves without being lowered to the ground. This lateral, spirally circular display has been observed in *heteropleura*, *heterochelos*, *stylifera*, *princeps*, *maracoani* and *insignis* (Text-fig. 2). It reaches its maximum development in the two latter species, which are allopatric counterparts in the Atlantic and Pacific. In both of them, which attain large size and a correlated remarkable development of the heterogonic major cheliped, the chelae are directed upward, spread wide apart and then rotated without pause, often for several minutes at a time. Even in their low intensity displays these two species are of the lateral type; in the others, however, low intensity waving shows single-plane, vertical-wave affinities. Most of the group hold the carapace high during a series of waves, although in *stylifera* and *princeps* the hind legs bend during the highest reach of the cheliped, tilting the posterior part of the carapace downward. *U. heteropleura*, *heterochelos* and young *princeps* raise and lower the carapace with each wave.

Two narrow-fronted crabs, the Australian *longidigitum* and the Indo-Pacific *tetragonon*, as well as the Indo-Pacific broad-fronted *gaimardi*, all show wave characteristics intermediate between the vertical and lateral types. The displays are very distinct, however, and the three species are not morphologically closely related to one another.

Alone among the known displays of broad-fronted crabs the neotropical Atlantic *thayeri* has a vertical, single-plane type of wave similar to those of the Indo-Pacific narrow-fronts. Morphologically, also, *thayeri* shows affinities with those species.

The remaining broad-fronts, in which display has been observed, are all characterized by a strongly lateral type of wave, usually with a variable degree of circularity (Text-fig. 3). In a number of the very rapidly waving neotropical broad-fronts, such as *beebei* and *saltitanta*, the last half of the wave is so swift that the eye does not record it. Hence although the motion was often described in field notes as a single-plane wave, subsequent examination of



TEXT-FIG. 1. Examples of vertical types of wave in three species of narrow-fronted *Uca* from the Indo-Pacific region. Illustrations on left show rest positions between waves, those on right the maximum elevation of the cheliped, which is raised and lowered in a single plane. Note in the series, reading from the top down, the progressively higher reach of the cheliped and greater elevation of the carapace. See text, p. 70 ff., Table 2 and Text-fig. 4, A-B.

A, B, *U. rhizophorae* (photographed in Singapore); C, D, *signata* (Philippine Is.); E, F, *zamboangana* (Philippine Is.). Drawings by Dorothy F. Warren, after motion picture frames and mounted specimens.

motion picture frames proved that circularity was clearly evident.

Examples of a strongly circular type of lateral wave include the Indo-Pacific *annulipes* and *lactea* (Text-fig. 3, A-D) and the eastern Pacific *latimanus*.

In a few species, such as *U. terpsichores*, the rest position of the cheliped during display is with the chelae directed forward.

An aberrant group of broad-fronts, of which *pugnax rapax* (Text-fig. 3, E-F) is typical, is an important element in neotropical *Uca*; two Atlantic representatives extend even into the north temperate region (*pugnax*, *minax*). They are all characterized by exceedingly broad fronts and

by a jerking, obliquely-lateral wave which during moderate intensity is circular. They have no Indo-Pacific representatives.

The lateral wave of the broad-fronts, in the progressively specialized species, shows increasing speed, maximum unflexing of the cheliped and more prolonged periods of time devoted to waving.

It has already been noted that in species in which waving is poorly developed (*rhizophorae*, *manii*, etc.) the body is raised scarcely or not at all during waving. In the majority of species, among both narrow-fronts and less advanced broad-fronts, the carapace is raised on the ambulatories and lowered with every wave. In some

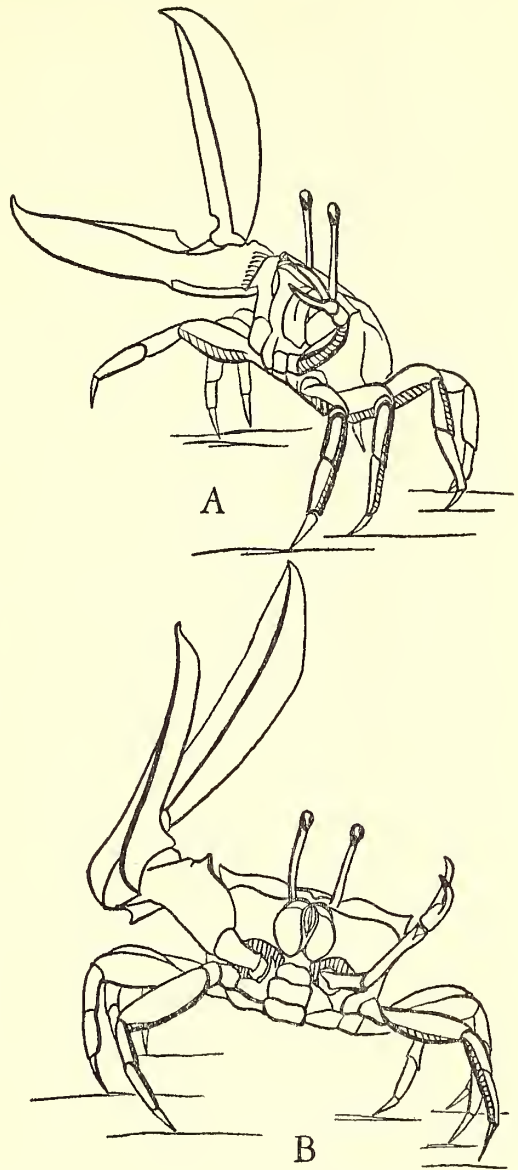
lateral wavers, the body is only slightly elevated, but is held in this position throughout the series. (In a few of this group, for example in *beebei*, an impression of raising-and-lowering is given by the tendency of the crab to bend the hind legs during the peak of the cheliped reach, thus tilting the carapace down posteriorly; this is especially true when the crab is displaying on soft mud; c.f. Peters, 1955, who reported that this form raises and lowers the carapace with every wave). In advanced species among both narrow-fronts and broad-fronts, the body is held high on the ambulatories throughout a series of waves.

IV. ADVANCED STAGES OF DISPLAY

One behavioral distinction between the narrow-fronts and the broad-fronts is found in all the species so far observed except for a few instances. This concerns the final stages of pre-mating behavior.

Advanced Display in Narrow-fronts. In the narrow-fronts the male pursues a female or approaches her at the mouth of her burrow; this behavior does not necessarily immediately follow display, although the male always has been displaying during the same low-tide period. The approach, however, often does follow display directed more or less toward a female, although this individual is not necessarily the one which is eventually approached. There is no marked increase in tempo of waving during the approach, and additional elements of display are lacking, except for a few special steps in the aberrant neotropical *stylifera*, *insignis* and *maracoani*. When within reach, the male seizes the female and, after brief tapping or stroking of her carapace with his ambulatories, attempts copulation at or near the mouth of her burrow. This has been observed by Altevogt (1955) in *marionis* in India; and by the present author as follows: *marionis* in Fiji, the Philippines, Australia and Singapore; *dussumieri* in the Philippines, Sarawak and Singapore; *manii* in Singapore and Penang; *rathbunae* in the Philippines; two undescribed new species in Australia; *heteropleura*, *stylifera* and *insignis* in Ecuador and Pacific Panama; and *maracoani* in Trinidad, northern South America and Brazil. Actual copulation was seen in *marionis* (four times), *rhizophorae* (twice), *manii* (twice), *dussumieri* (once), Australian new species (once) and *stylifera* (once). The last stage of courtship, involving stroking, has been observed probably 75 times at a conservative estimate, although these latter episodes did not, after display, end in copulation.

A few instances of apparently atypical behavior is known in the narrow-fronts. Females of *stylifera* (Crane, 1941, p. 172) *insignis* and



TEXT-FIG. 2. Lateral circular type of wave in the neotropical crab, *Uca insignis* (photographed in Panama). Carapace is held high on the ambulatories throughout a series of high-reaching circular waves, during which the cheliped is never brought down into the flexed position of rest. A, maximum reach of cheliped; B, "low" position, between waves. See text, p. 71, and Table 2. Drawings by Dorothy F. Warren after motion picture frames and mounted specimens.

signata were seen on one occasion each to follow a displaying male into his burrow. Two small *princeps* (*ibid*, p. 170) seized females. Each tried unsuccessfully to drag the female down

his own burrow, grasping her with the ambulatories of the minor side.

During all of the above instances where I have observed final stages of display and copulation above ground I have never once seen the male seize and hold the female with the major cheliped. Therefore the definite holding observed by Altevogt near Bombay in copulating *marionis* (1955.2, p. 518) apparently is of rather exceptional occurrence.

Advanced Display in Broad-fronts. In the broad-fronted group, in addition to an increased tempo of display at the approach of a female, there are specialized steps, curtsies or rappings which are only elicited at this time.

Another group distinction is apparent at the end of courtship. In the broad-fronts the usual procedure is for the male, after high intensity display, to precede the female down his own burrow; the female may or may not follow, and may or may not stay below, presumably copulating, for any length of time. I have seen the female actually follow the male into the burrow in the Indo-Pacific *annulipes* in Karachi, Singapore, Sarawak and Davao; in *lactea* in Pakistan, Singapore, the Philippines, and Fiji; in the Pacific neotropics in *stenodactyla*, *beebei*, *batuenta*, *salitanta* and *latimanus*; and, finally, in the western Atlantic in *pugnax*, *pugnax rapax*, *pugillator*, *cumulanta*, *leptodactyla* and in two apparently undescribed new species.

In only two broad-fronts, *stenodactyla* and *beebei* in Panama, was copulation seen; this was at the surface by the female's burrow as in narrow-fronts (Crane, 1941, pp. 193, 197). A number of females in each of these two species, however, have been seen to follow the male in the usual broad-front fashion. Throughout the broad-fronted group, therefore, underground mating in the male's burrow is presumably the rule and the female, instead of being pursued toward her own burrow by the male and often seized more or less forcibly, is attracted by rapid and characteristic display into the burrow of the male which she enters after he has disappeared.

In the broad-fronted *gaimardi* (= *pulchella* Stimpson) in Tahiti both the first and the last stages of display appear almost perfectly intermediate between those typical of the primitive narrow-fronts and of the broad-fronts. The intermediate character of the wave has already been mentioned; advanced stages of display were lacking and the male pursued the female as in narrow-fronted crabs. Even during high intensity display the carapace was scarcely elevated. Morphologically, as usual with crabs having intermediate displays, the species shows intermediate characters.

Another broad-fronted species of particular interest is *salitanta*, from the Pacific neotropics. As noted previously (1941, p. 166) this form represents the extreme in development of the rapping type of display, which occurs in a number of related species on both coasts of tropical America. In these species a crab, at the end of a wave, may bounce the lower edge of the major manus and pollex on the ground (Text-fig. 4 F). Usually this bouncing or rapping occurs only when the crab is excited, often in the final stages of courtship. It is typical immediately before the male's descent into his own burrow, after display has been directed toward a particular female. In *salitanta* the rapping has been pushed forward to become an integral part of routine waving, whether or not the crab is particularly excited and whether or not display has been directed toward a female.

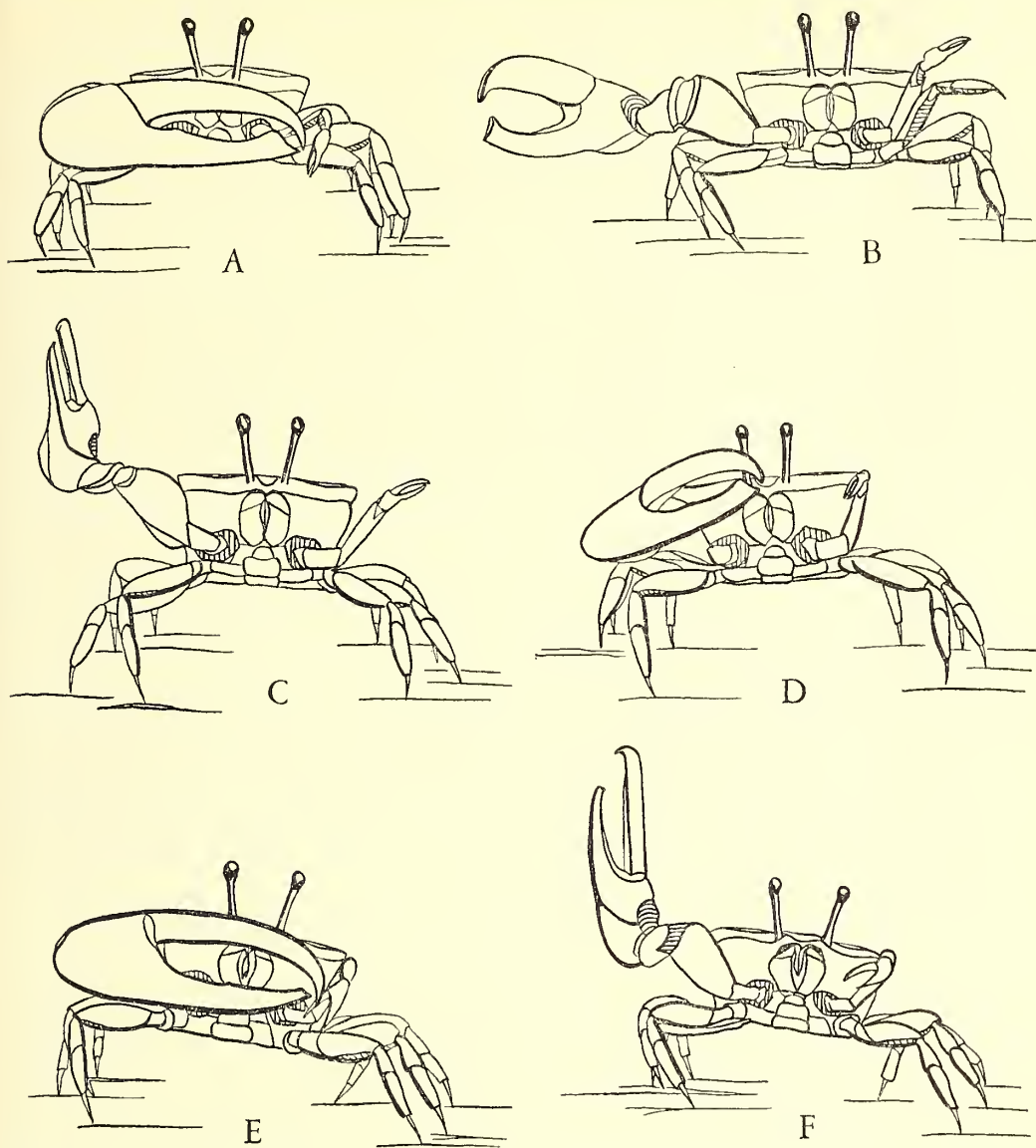
The basic characteristics of the lateral wave itself may be superseded during the specialized motions of advanced display. Depending on the species, the cheliped may be held motionless overhead, or in front, while the crab bobs and races to and fro. Again, the cheliped, having passed through stages of low-intensity single-plane and high-intensity circular display, reverts once more to a single-plane return; now, however, the cheliped is opened laterally and raised to maximum height while the waving tempo is greatly increased. In a number of species the cheliped is not returned to its usual rest position between waves, but performs an aerial circle, somewhat similar to that found in the aberrant neotropical narrow-fronts.

In Table 2 only a slight indication is given of the types of advanced display occurring among the broad-fronts. In spite of group similarities, the display of each species is so distinct that, if seen in moderate intensity and advanced stages, none could ever be confused in the field with that of any other species, even from other parts of the world.

As in studies of the complex displays of certain vertebrates, it is obviously essential, both for accuracy of description and for an approach to understanding, that the displays be observed for prolonged periods and under a variety of conditions.

V. ECOLOGICAL DIFFERENCES IN THE DISTRIBUTION OF DISPLAY TYPES

In 1941 (p. 160) the present investigator noted that the most highly developed displays in western Central American crabs were found in species living on the shores of bays and estuaries which, while protected from waves, were freely confluent with the open sea and consequently of



TEXT-FIG. 3. Examples of lateral types of wave in broad-fronted *Uca*. A-D, *U. lactea* (photographed in Fiji Is.), showing maximum development of the lateral circular wave, in which the cheliped starting from the flexed position (A) is unflexed outward (B), then raised (C), and finally returned (D) to the starting point. This wave is best developed in displays of moderate intensity; at low intensity or at high intensity during advanced display, the wave may be of a vertical or lateral single plane type. See text, p. 71, Table 2 and Text-fig. 4, C-E. E, F, *U. pugnax rapax* (Venezuela). Rest position and maximum cheliped reach of lateral circular wave, characteristic of moderate intensity display. Cheliped is unflexed outward, raised and lowered in a series of jerks. See text, p. 72, and Table 2. Drawings by Dorothy F. Warren, after motion picture frames and mounted specimens.

relatively high salinity. Recent observations in the Indo-Pacific have shown agreement. In both the narrow-fronted and broad-fronted groups the most actively displaying species, which apparently are also most morphologically advanced, are those in similar localities. Examples

of Indo-Pacific crabs with well developed displays are the narrow-fronts *marionis* and *tetragonon* and the broad-fronts *annulipes* and *lactea*; all live typically on rather open shores or inlets of protected bays, as do their neotropical counterparts including *insignis* and *maracoani* among

the narrow-fronts and *stenodactyla*, *deichmanni*, *terpsichores*, *latimanus* and *leptodactyla* among the broad-fronts. Those with the least developed displays, the Indo-Pacific *rhizophorae*, *manii*, etc. (p. 71), are also those morphologically the least specialized for an amphibious life; all inhabit less saline situations, sometimes living in almost fresh water, on more sheltered mudflats and streambanks.

An interesting point is that the extremely broad-fronted American group, including *pugnax* and *mordax*, has spread into sheltered localities extending even, in *mordax*, far up tropical rivers. The tempo of their displays is slow, as in sheltered, unrelated species in the Indo-Pacific, but it is clearly of the lateral, highly developed broad-fronted type, and the females, as usual in the broad-fronts, are attracted down the burrows of the males.

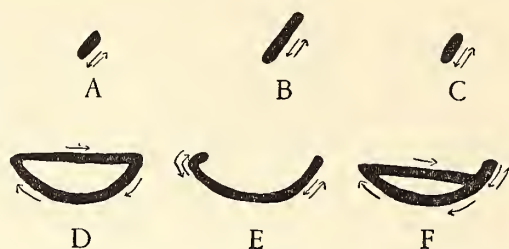
VI. GEOGRAPHICAL DISTRIBUTION IN RELATION TO DISPLAY

Those narrow-fronted species with the simplest and apparently most primitive display (*manii*, etc.) are all confined to the Indo-Malayan region, which undoubtedly is the center of distribution for the family. The intermediate narrow-front, *tetragonon*, which currently reaches Tahiti and was formerly found also in Hawaii, shows in its display as in its morphology certain intermediate elements which seem to form a link with the American narrow-fronts. The displays of the latter are more highly evolved than any yet known in the group in the Indo-Pacific, and show affinities to those of the broad-fronts; the species are also specialized morphologically, being characterized for example by extreme narrowness of the front, by unique peculiarities of the spoon-tipped hairs of the second maxilliped, and by male abdominal appendages more similar to those of broad-fronts than of Indo-Pacific narrow-fronts.

The broad-fronted displays are represented by both simple and advanced examples in both hemispheres. There are, however, many more American than Indo-Pacific species, and most of the American species are more specialized in both behavior and morphology than any of the observed Indo-Pacific broad-fronts with the exception of *lactea*.

U. gaimardi, the only Indo-Pacific broad-front reaching as far east as Tahiti, appears to be, as is *tetragonon* among the narrow-fronts, an intermediary between Indo-Pacific narrow-fronts and American broad-fronts.

Three Indo-Pacific species have been observed in display over a horizontal distribution of 5,000 to 8,000 miles. These are *marionis*, *annulipes*



TEXT-FIG. 4. Ground projection of path of various types of wave in *Uca*. In each path the beginning is at upper right boundary of the black line. In A, B and C, the length of the line represents the extent of the obliquely forward thrust of the cheliped during its elevation. A, *U. rhizophorae*, a low vertical wave, single plane; B, *zamboangana*, a high vertical wave, single plane; C, *lactea*, a vertical, single plane wave occurring in low intensity display; D, same, a lateral circular wave, typical of display of moderate intensity; E, same, a lateral, single-plane wave found during advanced stages of display; F, *saltitanta*, a lateral circular wave, with straight line marking route as cheliped retraces beginning of path, rapping ground in front of crab as the claw bounces back into rest position. Cf. text, p. 70, and Text-figs. 1 and 3.

These projections were obtained by placing a preserved, flexible specimen of each species on a thick sheet of modelling clay and fastening a needle to the tips of the major chelae with scotch tape in such a way that, regardless of the elevation of the cheliped, the needle cut partially through the modelling clay. Starting from the flexed, rest position the cheliped was then moved as though in natural display, in accordance with motion picture records, the tip of the needle marking the projected path.

and *lactea*. No gross variations in display behavior have been observed among the various populations within each species, although detailed analyses of motion picture film are expected to show minor distinctions. The one major difference, noted among the populations of *lactea*, was that no "shelters" (Crane, 1941, p. 157) were built by the species even at the height of display in Singapore, the Philippines or Fiji. They were, however, built by about one-fourth of the adult male *lactea* in Karachi, Pakistan, in mid-June.

VII. EVOLUTIONARY TRENDS

The varying patterns of *Uca* display, from the simplest to the most complex, show a trend prevalent in many branches of the animal kingdom in groups where vision is well developed. In *Uca*, as in numbers of birds, reptiles, fishes, spiders and mantids, for example, it is axiomatic that the display increases the conspicuousness of the animal—regardless of the function of the particular display under consideration.

A primary component of the conspicuousness is usually a temporary or apparent increase in size. In fiddler crabs this increase is attained in three ways; first by a progressively higher reach with the cheliped; second by the broadening of the wave into an expansive lateral gesture replacing a close-to-the-body motion; and, third, by the higher and more prolonged elevation of the body on the increasingly straightened walking legs. In some advanced laterally-waving species, however, the body is not held very high, the walking legs being braced far out at the sides; this position seems to be an aid in balancing. It is probably a necessary stance in these species in which both heterogony and the lateral extension of the cheliped are extreme.

There are other display characteristics which contribute to the conspicuousness of the crab and which are attained most fully in those species in which waving is highly developed. These characteristics include faster tempo of the wave, a rhythm accented by jerks or other specializations and an increase in time devoted daily to waving.

The trend toward the attraction of females to the male burrow, typical of the broad-fronts, may well have adaptive value, since pairs copulating at the surface are fully exposed to predation by birds. A probable factor in the evolution of this pattern is the fact that among broad-fronts the male is often considerably larger than the female. Because of this size discrepancy males cannot easily descend into the narrow burrows of the females.

Many species with highly developed displays resemble primitive forms when waving at low intensity. This is especially well shown when a crab is feeding and waving at the same time, when tidal or meteorological conditions are unfavorable, or when the crab is not physiologically in full display condition. Under any of these circumstances even species as far apart phylogenetically as *maracoani*, *stenodactyla* and *lactea* may raise the cheliped only slightly and lower it in the same, nearly vertical plane, scarcely elevating the body. This low intensity display therefore is very similar to the full display of *rhizophorae*, *manii* and their relations.

There appear to be no structural reasons preventing vertical wavers from displaying in the lateral fashion. The form of the condyles, the proximal concavities of articulating segments and the elasticity of the connections are similar throughout, although Peters (1955, pp. 489 ff.) illustrates minor differences in the degrees of possible motion in two closely related species. Throughout the genus the cheliped is often widely extended, regardless of the type of wave performed during display, in combat between males

when the chelae of the combatants are actually engaged.

Altevogt (1955.2, p. 514) recorded differences in the display of very large and moderate-sized individuals of *marionis*, the giants having a less out-reaching form. He thinks this is probably associated with the altered center of gravity. It seems to the present investigator that the evolution of the form of display in the gigantic species of neotropical narrow-fronts, *maracoani* and *insignis*, may have been guided by similar problems of weight and balance.

Evidence has recently been found that displacement behavior sometimes occurs during *Uca* display, and it seems likely that such behavior varies among the species roughly in accordance with their phylogenetic position. Gordon (1955) first reported displacement feeding (in the sense in which the term has been used by Armstrong, 1950, and Tinbergen, 1952) in a number of African species. I fully agree with her interpretation, having often observed similar types of activity not only in *Uca* but in other genera of displaying ocypodids, notably *Ilyoplax*.

Gordon's observations were of feeding, often in a token, non-functional fashion, usually after fighting or after high intensity display and a thwarting of mating behavior.

The current studies present evidence of two more aspects of the subject. First, displacement behavior is most prevalent in species characterized by highly developed display. Second, in these species there occurs not only displacement feeding, as described by Gordon, but also displacement claw-cleaning. The large manus and chelae are buffed and polished by the small, or at least the requisite motion is made, although the terminal brush may not actually touch the large chelae. The gesture is repeated frequently even though the crab has been above ground for many minutes and the cheliped is altogether free of mud. This activity seems to occur especially when there is conflict between the urge to display and that to escape, such as when the camera or observer is very close to the crab.

Current observations indicate furthermore that there will prove to be specific differences in the tendency toward one type or another of displacement behavior. For example, *festae* in Ecuador, *deichmanni* in Panama and *cumulanta* in Trinidad and Venezuela all appear to be especially prone to displacement claw-cleaning. *U. lactea* in the Indo-Pacific and *leptodactyla* in Brazil, on the other hand, seem to have a stronger tendency to displacement feeding. In contrast, in the primitive Indo-Pacific narrow-fronts (*rhizophorae* et al.) no displacement behavior has been noticed; it appears likely that in these

TABLE 1. SPECIES OF *Uca* IN WHICH DISPLAY HAS BEEN STUDIED DURING THE PRESENT INVESTIGATION

Note: The majority of these forms are undoubtedly good species. It is expected that some will be reduced to subspecific rank, especially certain narrow-fronted crabs with narrow ranges in the Indo-Pacific. This however does not alter the fact that the displays of all the forms listed below are distinct.

The 43 species are arranged alphabetically since a phylogenetic presentation must await the publication of correlated morphological evidence. Display has also been observed in at least ten additional species; since these are apparently new and undescribed, they have been omitted from the list. Motion picture records have been obtained of more than three-quarters of all the species observed.

In the second column are given references to descriptions of waving published after 1940. An account of earlier work on *Uca* display is given in Crane, 1941, p. 152. Since these early reports lacked a comparative ethological viewpoint they remain, for present purposes, chiefly of historical interest and will not be repeated here. The only references included below, therefore, are recent wave descriptions which are to some degree specifically diagnostic. Published records which are extremely incomplete (e.g. of *minax*, Crane, 1944) are omitted, as are displays not described but mentioned in connection with another subject (e.g. Gordon, 1955, on displacement behavior).

In addition to the displays listed below which Peters (1955) has also recorded, he has described (*loc. cit.*) those of *macrodactyla glabromana* Bott and *leptochela* Bott, neither of which species has been observed by the present author. Hediger (1934) gives a helpful account of *tangeri* in a reference inadvertently omitted by Crane, 1941.

Species	Description of waving since 1940	General Range	Localities where display was observed by author
<i>annulipes</i> (Latreille)	---	Indo-Pacific	Pakistan (Karachi), Ceylon, Penang, Singapore, Sarawak, Philippines
<i>batuenta</i> Crane	Crane, 1941 Peters, 1955	E. Pacific	Panama, Ecuador
<i>beebei</i> Crane	Crane, 1941 Peters, 1955	E. Pacific	Panama, Ecuador
<i>cumulanta</i> Crane	Crane, 1943	W. Atlantic	Venezuela, Trinidad
<i>deichmanni</i> Rathbun	Crane, 1941	E. Pacific	Panama
<i>dussumieri</i> (Milne Edwards)	---	Indo-Pacific	Singapore, Sarawak, Philippines
<i>festae</i> Nobili	---	Ecuador	Ecuador
<i>gaimardi</i> (Milne Edwards)	---	Western & Central Pacific	French Oceania (Tahiti, Raiatea, Bora Bora)
<i>galapagensis</i> Rathbun	---	E. Pacific	Ecuador
<i>heterochelos</i> (Lamarck)	---	W. Atlantic	Venezuela
<i>heteropleura</i> (Smith)	Crane, 1941	E. Pacific	Panama, Ecuador
<i>inaequalis</i> Rathbun	Crane, 1941 Peters, 1955	E. Pacific	Panama, Ecuador
<i>insignis</i> (Milne Edwards)	---	E. Pacific	Panama, Ecuador
<i>inversa</i> (Hoffmann)	---	Indo-Pacific	Pakistan (Karachi)
<i>ischnodactyla</i> Nemece	---	Fiji	Fiji
<i>lactea</i> (de Haan)	---	Indo-Pacific	Pakistan (Karachi), Singapore, Philippines, Fiji, Samoa
<i>latimana</i> (Rathbun)	Crane, 1941 Peters, 1955	E. Pacific	Panama, Ecuador
<i>leptodactyla</i> (Guérin)	---	W. Atlantic	Venezuela, Brazil
<i>linicola</i> Crane	---	E. Pacific	Panama
<i>longidigitum</i> (Kingsley)	---	E. Australia	Nr. Brisbane

TABLE 1. SPECIES OF *Uca* IN WHICH DISPLAY HAS BEEN STUDIED DURING THE PRESENT INVESTIGATION
(Continued)

Species	Description of waving since 1940	General Range	Localities where display was observed by author
<i>manii</i> Rathbun	—	Indo-Pacific	Singapore
<i>maracoani</i> (Latreille)	Crane, 1943	W. Atlantic	Venezuela, Trinidad, British Guiana, Surinam, Brazil
<i>marionis</i> (Desmarest) (incl. <i>nitida</i> (Dana))	Altevogt, 1955.1, 1955.2	Indo-Pacific	Singapore, Sarawak, East & North Australia, Philippines, Fiji
<i>minax</i> (Le Conte)	—	W. Atlantic	New Jersey
<i>mordax</i> (Smith)	Beebe, 1928 Crane, 1943	W. Atlantic	Guatemala, Venezuela, Trinidad, Brazil
<i>oerstedii</i> Rathbun	Crane, 1941	E. Pacific	Panama
<i>olympioi</i> Oliveira	—	S. Brazil	Rio de Janeiro
<i>panamensis</i> (Stimpson)	—	E. Pacific	Panama
<i>princeps</i> (Smith)	Crane, 1941 Peters, 1955	E. Pacific	Panama, Ecuador
<i>pugilator</i> (Bosc)	Crane, 1944 Burkenroad, 1947	W. Atlantic	Connecticut, New York, Florida
<i>pugnax</i> (Smith)	Crane, 1944	W. Atlantic	Massachusetts, Connecticut, New York, Florida
<i>pugnax rapax</i> (Smith)	Crane, 1943	W. Atlantic	S. Florida, Guatemala, W. Indies, Colombia, Venezuela, British Guiana, Surinam, Brazil
<i>rathbunae</i> Pearse	—	Philippines	Manila, G. of Davao
<i>rhizophorae</i> (Tweedie)	—	Malaya & Borneo	Singapore, Sarawak
<i>rosea</i> (Tweedie)	—	Malaya	Penang
<i>saltitanta</i> Crane	Crane, 1941 Peters, 1955	E. Pacific	Panama
<i>signata</i> (Hess)	—	Indo-Pacific	Australia (Gladstone), Philippines
<i>speciosa</i> (Ives)	—	W. Atlantic	S. Florida
<i>stenodactyla</i> (Milne Edwards & Lucas)	Crane, 1941 Peters, 1955	E. Pacific	Costa Rica, Panama, Ecuador
<i>stylifera</i> (Milne Edwards)	Crane, 1941	E. Pacific	Panama, Ecuador
<i>terpsichores</i> Crane	Crane, 1941	E. Pacific	Panama, Ecuador
<i>tetragonon</i> (Herbst)	—	Indo-Pacific	French Oceania (Bora Bora)
<i>thayeri</i> Rathbun	—	W. Atlantic	Trinidad, Brazil
<i>zamboangana</i> Rathbun	—	Philippines	Gulf of Davao

species display is so feebly developed that, when any conflict or frustrating situation arises, the crab simply stops waving.

No comment can yet be made on the role displacement behavior, through ritualization,

may have played in the evolution of display motions.

Studies on heliconiid butterflies in Trinidad (Crane, 1955 and in ms.) apparently show conclusively the frequent occurrence of displace-

TABLE 2. ARRANGEMENT OF *Uca* spp. ACCORDING TO GENERAL TYPE OF WAVE.

Key: Species names in <i>italics</i> : narrow-fronts.		Species names in bold-face : broad-fronts.
IP: Indo-Pacific.		} general type of outstanding characteristic in advanced display.
EP: Eastern Pacific.		
WA: Western Atlantic.		
No AD: No special advanced display characteristics.		
(Where distribution symbol is not followed by one of these key designations, advanced display is incompletely known. See text).		
	Wave Vertical	Wave Lateral
Body position at moderate display intensity	(Cheliped raised upward at beginning of wave; always returned to position in same plane)	(Cheliped extended to side at beginning of wave; often returned to position via a circular route)
Body raised throughout a series of waves	<i>zamboangana</i> (IP)	<i>annulipes</i> (IP) (curtsy) <i>beebei</i> (EP) (special steps) <i>festae</i> (EP) (special steps) <i>galapagensis</i> (EP) <i>inversa</i> (IP) <i>lactea</i> (IP) (curtsy) <i>latimanus</i> (EP) (curtsy) <i>leptodactyla</i> (WA) (curtsy) <i>limicola</i> (EP) <i>minax</i> (WA) <i>mordax</i> (WA) (curtsy) <i>olympioi</i> (WA) (curtsy) <i>pugnax</i> (WA) (curtsy) <i>stenodactyla</i> (EP) (special steps) <i>terpsichores</i> (EP) (special steps) <i>insignis</i> (EP) (special steps) <i>maracoani</i> (WA) (special steps) <i>princeps</i> (EP) <i>stylifera</i> (EP) (special steps)
Body conspicuously raised and lowered with each wave.	<i>dussumieri</i> (IP) (No AD) <i>marionis</i> (IP) (No AD) <i>signata</i> (IP) (No AD) thayeri (WA) (No AD)	batuenta (EP) (rapping) cumulanta (WA) (rapping) deichmanni (EP) (rapping) inaequalis (EP) (rapping) cerstedti (EP) panamensis (EP) pugilator (WA) (rapping) saltitanta (EP) (rapping) speciosa (WA) (rapping) <i>heterochelos</i> (WA) <i>heteropleura</i> (EP) (No AD)
Body not raised, at all, or minimally raised and lowered with each wave.	gaimardi (IP) (No AD) <i>longidigitum</i> (Australia) <i>tetragonon</i> (IP) (No AD) <i>ischnodactyla</i> (IP) (No AD) <i>manii</i> (IP) (No AD) <i>rathbunae</i> (IP) (No AD) <i>rhizophorae</i> (IP) (No AD) <i>rosea</i> (IP) (No AD)	

ment behavior in these insects. Its probable occurrence has been mentioned in salticid spiders (*idem*, 1948, p. 202), mantids (*idem*, 1952, p. 288) and *Drosophila* (Bastock & Manning, 1955, p. 104). It now seems likely that displacement behavior will prove to be a noteworthy factor in the ethological study of many higher invertebrates.

VIII. SUMMARY

Two basic patterns of display have been distinguished during field studies of more than fifty species of fiddler crabs (*Uca*). The first pattern is characteristic of a group of species with narrow fronts. It is distinguished by a simple, more or less vertical gesture ("wave") made with the major cheliped of the male, and by the male's pursuit of the female toward her burrow; copulation in the known instances takes place on the surface of the ground. The second pattern is typical of broad-fronted species in the genus. It is characterized as follows: the cheliped is unflexed laterally, rather than vertically elevated, and sometimes completes a circular motion in returning to rest position; there is in addition a distinct second stage of display which is usually elicited by the approach of a female and which depends both on special movements of the various appendages and on an increased tempo of waving; finally, in the last stage of display the male attracts the female down his own burrow, which he enters first. A few species with intermediate types of behavior have been observed, especially in the Indo-Pacific.

The simplest and most primitive of the narrow-fronted displays are found in a group of closely related Indo-Pacific species of narrow distribution which inhabit protected estuaries and tidal streams; *manii* and *rathbunae* are examples. Displays of higher development are found among species inhabiting more saline, exposed locations; typical of these are *tetragonon* and *zamboangana*, both from the Indo-Pacific area. The narrow-fronted crabs reach their highest display development, along with their greatest morphological specialization, in the neotropical representatives, culminating in *insignis* and *maracoani*. All favor relatively exposed habitats.

The broad-fronted, laterally waving fiddler crabs are distributed in both the Indo-Pacific and American regions but, unlike the narrow-fronted species, they are poorly represented in the Indo-Pacific. As in the other groups, the highest display development occurs among species living in more seaward niches. Representatives are found of both simple and highly evolved displays. As examples, *gaimardi*, from the western

and central Pacific, illustrates the simplest known type of lateral display, while complex specializations are shown variously by *lactea* from the Indo-Pacific, *salitanta* and *terpsichores* from the eastern Pacific and *pugnax* from the western Atlantic.

Three wide-ranging Indo-Pacific species have been observed in display over distances ranging from 5,000 to 8,000 miles. No gross intraspecific differences were noted on the peripheries or elsewhere in their ranges, except that some displaying *lactea* built small structures of sandy mud in Karachi, but not in either the Philippines or the Fiji Islands, at least during the period of observation.

As is usual in a number of animals, the general trend in display evolution in *Uca* is toward increased conspicuousness. This increase is attained principally by higher speed in waving, by greater complexity in the rhythms and forms of display motions and by increased apparent size, through extension of the appendages either vertically or horizontally. The species in which display is highly evolved also spend a greater portion of their time in display than do other members of the genus.

Displacement behavior during *Uca* display is briefly discussed, including its possible role in the systematics of the group.

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EXPLANATION OF THE PLATE

PLATE I

Oblique views of different types of wave in fiddler crabs. For comparison with frontal views, Text-figs. 1 and 3.

FIG. 1. Vertical wave: *Uca dussumieri* displaying near Sasa, Gulf of Davao, Philippine Islands. Maximum elevation of cheliped.

FIG. 2. Vertical wave: *Uca marionis* in Singapore.

Major cheliped partially elevated. Note forward direction of merus and carpus, and compare their position in Fig. 4, below.

FIG. 3. Lateral wave: *Uca latimanus* near Panama City, Panama. Maximum elevation of cheliped.

FIG. 4. Lateral wave: *Uca annulipes* near Santobong, Sarawak. Cheliped partially elevated. Note lateral direction of merus and carpus.



FIG. 1



FIG. 2



FIG. 3



FIG. 4

BASIC PATTERNS OF DISPLAY IN FIDDLER CRABS (OCYPODIDAE, GENUS UCA)



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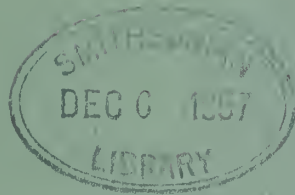
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Studies on the Lizard Family Xantusiidae. III. A New Genus for *Xantusia riversiana* Cope, 1883

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(Text-figures 1-3)

IN the course of investigations leading toward a complete revision of the night lizard family Xantusiidae, it has become apparent that *Xantusia riversiana* Cope, 1883, is so different from other members of the group that a new genus is required for its reception. The decision to place *riversiana* in a separate genus is based upon an analysis of the scutellation, body proportions, coloration, life history and habits of all known xantusiids, combined with an extensive study of the osteology of the family. Detailed consideration of these features, characterization of the genera and species of xantusiids and discussion of the evolutionary patterns within the family are reserved for the revisional report. However, it seems advisable to propose the new genus in advance of the appearance of the larger work in order to make the name available to others investigating various aspects of the biology of the Xantusiidae. To increase the usefulness of the present paper an artificial key to the genera of night lizards is appended to the description of the new genus.

There has been considerable confusion in the past concerning the status and relationships of several genera and species of Xantusiidae because of the lack of a standardized terminology for the squamation of these lizards. In order to analyze the scutellational differences and similarities among members of the family it has been necessary to revise completely the existing system employed for the scales on these lizards. A detailed discussion and definition of scutellational terms will be included in my revision of the family, but for the sake of consistency the new system of scale terminology is used throughout the

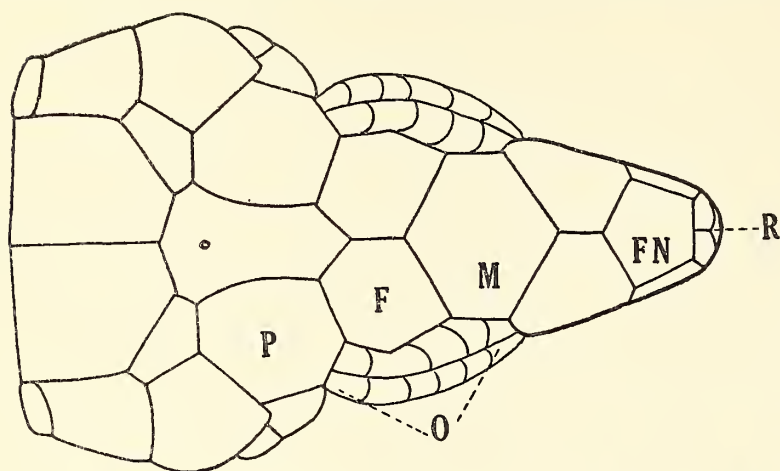
present report. The head shields of *riversiana* are illustrated in Text-figures 1-3. The terms radials and femorals refer to the scales along the anterior surface of the forearm and thigh, respectively. Walker (1955) has utilized my system of scale nomenclature in his descriptions of new *Lepidophyma* from Mexico.

It is a great pleasure to have the opportunity of naming what may well be the last new genus of recent reptiles from western North America in honor of Dr. Laurence M. Klauber of San Diego, who has contributed so magnificently to our understanding of the herpetofauna of this region.

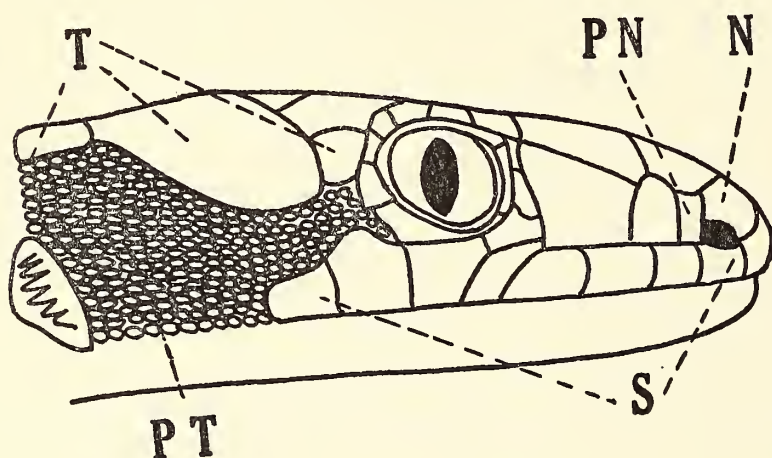
Klauberina, new genus

Type of Genus.—*Xantusia riversiana* Cope, 1883.

Definition.—*External characteristics:* (1) one frontonasal; (2) a large median; (3) two frontals; (4) two parietals; (5) no pretemporals; (6) temporals a series of enlarged plates; (7) two rows of supraoculars; (8) nostrils pierced at juncture between nasal, postnasal, rostral and first supralabial; (9) pretympans granular; (10) postmentals and infralabials distinct; (11) anterior postmentals paired; (12) anterior pre-gulars granular; (13) gulars enlarged rectangular plates, much larger than pre-gulars; (14) dorsal scales granular; (15) dorsals essentially homogeneous in size and shape; (16) ventrals in 16 longitudinal rows; (17) radials and femorals forming enlarged plates; (18) caudals faintly keeled; (19) all scales in caudal whorls of same size. *Osteological characteristics:* (20) nasals meeting one another for most of their length;



TEXT-FIG. 1. Diagram of dorsal head scutellation of *Klauberina riversiana* (Cope, 1883). R = rostral; FN = frontonasal; M = median; F = frontal; P = parietal; O = supraocular series.



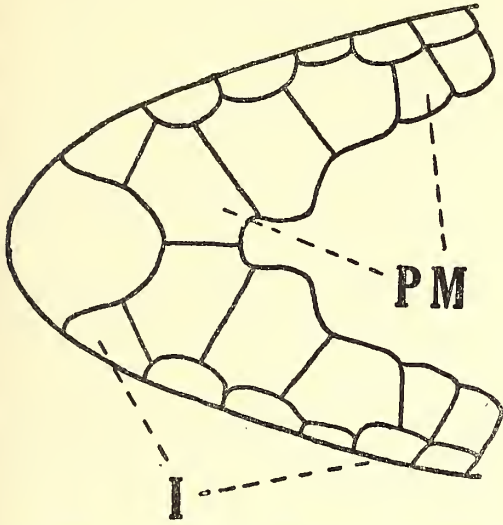
TEXT-FIG. 2. Diagram of lateral head scutellation of *Klauberina riversiana* (Cope, 1883). N = nasal; PN = postnasal; PT = pretemporals; S = supralabial series; T = temporals.

(21) premaxillary not reaching to frontals; (22) frontals paired; (23) frontals not roofing over orbits above, outer margins concave; (24) parietals paired; (25) squamosal touching parietal; (26) prefrontal extending onto top of skull, excluding a portion of frontal from orbit; (27) jugal moderately broad; (28) postfronto-orbital not expanded medially, gradually decreasing in width from anterior to posterior; (29) anterior bony palate of paleochoanate type; (30) fenestra vomeronasalis externa bordered by prevomer and maxillary; (31) epipterygoid process from prootic; (32) ectopterygoid and palatine in contact or narrowly separated; (33) basisphenoid and basioccipital distinct; (34) teeth on both jaws strongly triconodont; (35) clavicles perforate; (36) sternum without posterior projection; (37) phalangeal formula of hand 2-3-4-5-3.

Diagnosis.—The new genus may be readily separated from *Cricosaura* Gundlach & Peters, 1863, and *Lepidophyma* Auguste Duméril, 1851 (including *Gaigeia* H. M. Smith, 1939), by the

characters presented in the accompanying key. In addition *Klauberina* is distinct from these genera in a number of the features mentioned in the definition above (from *Cricosaura* in characters 1-5, 8-9, 11-12, 14-16, 18-22, 24-25, 27-32, 34-37, and from *Lepidophyma* in 5, 7, 8, 10-11, 13, 15-17, 23, 26-28, 34), but a complete summary of the differences between the various genera will be given elsewhere.

From its nearest ally, *Xantusia* Baird, 1859, *Klauberina* is distinguished by having (characters for *Xantusia* given in parentheses): **external**: no pretemporal scales (pretemporals present); temporals formed of a series of enlarged plates (temporals formed of small granules); two rows of supraoculars (one row of supraoculars); ventral scales in 16 longitudinal rows (ventrals in 12-14 rows); caudal scales slightly keeled (caudals smooth); **osteological**: jugal moderately broadened (jugal reduced to a narrow sliver); ectopterygoid and palatine in contact or nearly meeting (ectopterygoid and palatine widely



TEXT-FIG. 3. Diagram of squamation on underside of head of *Klauberina riversiana* (Cope, 1883). I = infralabials; PM = postmentals. The preular scales are the small scales lying median and posterior from the postmentals and anterior to the gular fold; the gulars are the scales on the gular fold.

separated); teeth strongly triconodont (teeth simple).

Klauberina riversiana is markedly different from the recently described Eocene fossil xantusiid, *Palaeoxantusia fera* Hecht, 1956, based upon a portion of a lower jaw from Elk Mountain, Wyoming (Bridger Formation), in having strongly triconodont teeth. The fossil genus has simple rounded teeth.

The nominal night lizard genus *Impensodens* erected on the basis of an incomplete lower jaw from Post-Pleistocene deposits in Yucatan, México (Langebartel, 1953), appears to be synonymous with *Lepidophyma* according to Hecht (1956, p. 3). In any event this mandible is distinct from that of *Klauberina* in having weakly triconodont teeth with the secondary cusps located on the inner surface of the teeth and not in the same longitudinal plane as the primary median cusp. *Klauberina* is distinctive within the family in having strongly triconodont teeth with all the cusps on a given tooth located along the same longitudinal plane.

Included Species. — *Klauberina riversiana* (Cope, 1883) of the California Channel Islands, Santa Barbara, San Clemente and San Nicholas, is the unique member of the genus.

Notes on the Family.—In a recent discussion of the position of the Xantusiidae within the suborder Sauria, McDowell & Bogert (1954, pp. 94-98) acknowledge the aid of my unpublished

study on the family as a source for certain of their remarks. Unfortunately the information presented by them cannot be derived from the data provided by me. Corrections therefore seem in order.

McDowell & Bogert state that among other features the family Xantusiidae is characterized by paired parietal bones, absence of a parietal foramen and ovulation involving but two eggs at one time (with rare exceptions). Contrary to these statements, one xantusiid, *Cricosaura typica* Gundlach & Peters, 1863, has the parietal bones fused to form a single element. Neither can the family be characterized as lacking a parietal foramen. Members of the genus *Xantusia* always have this aperture and *Klauberina* also consistently has the foramen (as clearly shown on figure 25 in McDowell & Bogert), although it may be partially or entirely covered by osteoderms on the outer surface of the skull in adult examples. The published studies of Brattstrom (1951) and Shaw (1949) conclusively show that *Klauberina* may produce four to ten ova at one time and my own investigations indicate that *Lepidophyma* usually has about six eggs formed at one period of ovulation. The species of *Xantusia* produce one to three ova but the usual number is two. In addition to these points, it may be noted that postanal bones and sacs are present in males of both *Xantusia arizonae* Klauber, 1931, and *Xantusia vigilis* Baird, 1859, not in *vigilis* alone as stated by McDowell & Bogert.

AN ARTIFICIAL KEY TO THE RECENT GENERA OF NIGHT LIZARDS

- 1a. A single frontal scale; no parietal scales; a single anterior postmental scale; nasal bones completely separated from one another by nasal process of premaxillary; frontal bone single; parietal bone single; phalangeal formula of hand 2-3-4-4-3. . . . *Cricosaura*
- 1b. Two frontal scales; two parietal scales; a pair of anterior postmentals or postmentals fused with infralabials; nasal bones in contact with one another for most of length; two frontals; two parietals; phalangeal formula of hand 2-3-4-5-3.
 - 2a. Supraoculars well-developed; postmentals and infralabials distinct; scales on back and sides essentially homogeneous in size and shape; radials and femorals enlarged into plates; orbit not completely roofed over above by frontal bone, outer margin of frontal concave; prefrontal bone extending onto top of skull, separating anterior portion of frontal from orbit;

postfronto-orbital not expanded medially, gradually decreasing in width posteriorly.

- 3a. No pretemporal scales; temporal scales enlarged plates; two rows of supraoculars; ventrals in 16 longitudinal rows; jugal expanded; ectopterygoid and palatine in contact or narrowly separated from one another; teeth triconodont. *Klauberina*
- 3b. Pretemporals present; temporals small, granular; one row of supraoculars; ventrals in 12-14 longitudinal rows; jugal reduced to a narrow sliver; ectopterygoid and palatine widely separated; teeth simple. . . . *Xantusia*
- 2b. Supraoculars reduced to a fleshy flap projecting from side of frontal scale; postmentals and infralabials fused into a single series; scales on back and sides a heterogeneous mixture of granules and enlarged scales; radials and femorals not enlarged, same size as other scales on limbs; orbit completely roofed over above by frontal bone, outer margin of frontal even, not concave; prefrontal bone not extending onto top of skull, not separating anterior portion of frontal from orbit; postfronto-orbital expanded medially, not gradually decreasing in width posteriorly. *Lepidophyma*

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Nesting Behavior of the Crested Oropéndola (*Psarocolius decumanus*) in Northern Trinidad, B.W.I.¹

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(Plates I & II; Text-figures 1-3)

[This paper is one of a series emanating from the tropical Field Station of the New York Zoological Society, at Simla, Arima Valley, Trinidad, British West Indies. This station was founded in 1950 by the Zoological Society's Department of Tropical Research, under the direction of Dr. William Beebe. It comprises 200 acres in the middle of the Northern Range, which includes large stretches of undisturbed government forest reserves. The laboratory of the station is intended for research in tropical ecology and in animal behavior. The altitude of the research area is 500 to 1,800 feet, with an annual rainfall of more than 100 inches.]

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INTRODUCTION

THE oropéndolas or giant caciques constitute an assemblage of neotropical birds, within the family Icteridae, made up of five genera (*Ocyalus*, *Zarhynchus*, *Chypicterus*, *Gymnostinops* and *Psarocolius*) and 12 species. They are among the largest passerine birds of the New World tropics, reaching 21 inches in

length, and are characterized by similar social habits, colonial nesting, vocalizations and display patterns. Their dominant colors are shades of black and brown with yellow or orange characteristically present in the tail and bill. Another closely related group of icterids are the true caciques (i.e., *Cassiculus* spp.) which, although quite similar in habits and appearance to the oropéndolas, average smaller in size. Previous studies on the 12 species comprising the oropéndolas have been limited to the life history studies of the Wagler Oropéndola (*Zarhynchus wagleri*) by Chapman (1928) and the Montezuma Oropéndola (*Gymnostinops montezuma*) by Skutch (1954).

The Crested Oropéndola or Giant Crested Cacique (*Psarocolius decumanus insularis*) is uniform brownish-black in general coloration, becoming chestnut on the rump and under tail coverts; the tail is lemon yellow with the middle pair of rectrices brownish-black; the bill pale greenish-yellow; the tarsi and toes black and the iris blue. The sexes are similar in color but differ in size, the female averaging 13 inches in length and the male 17 inches. Five subspecies of this oropéndola are recognized, ranging from Panamá across northern South America south to southern Brazil, Paraguay, northeastern Argentina, eastern Peru and eastern Bolivia. The race *insularis* is restricted to the islands of Trinidad and Tobago and northeastern Venezuela. The genus *Psarocolius* also includes the Green Oropéndola (*P. viridis*), the D'Orbigny Oropéndola (*P. atro-virens*) and the Chestnut Oropéndola (*P. angustifrons*).

Two nesting colonies of the Crested Oro-

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péndola were discovered in early January, 1955, in the cocoa plantation and secondary forest near Simla about four miles north of the town of Arima in the Northern Range of Trinidad. This area is situated in the Arima Valley at an elevation of 800 feet, and is bordered by lower montane rain forest which was, in all probability, the original forest type of the study area. For further ecological details of meteorology and biotic zones of this region see Beebe (1952). Both nesting sites were established in long-boled mountain immortelle or erythrina trees (*Erythrina micropteryx*) with the sack-like nests hanging some 60 to 80 feet from the ground. These immortelles are familiar nesting sites of the Crested Oropéndola in the Arima valley, and are common trees on the cocoa plantations where they were originally introduced as cover for the cocoa.

The birds were still in the process of nest-building when their sites were found. A blind was constructed on a slope opposite the more accessible colony (Colony A) at a level with most of the nests and about 100 feet away. This colony was visited daily from Jan. 12 to March 29 for a total of 303 hours. The second colony (Colony B), about a quarter of a mile from the first, was visited weekly from Feb. 6 to April 3 for a total of 15 hours. Observations were made with the aid of 7 X 50 binoculars, and moving pictures and photographs of special activities were taken through a six-inch or 300 mm. telephoto lens. The majority of the observation periods took place between 9:00 A.M. and noon in the morning and 2:30 P.M. to 6:00 P.M. in the afternoon. However, a number of observations were also made between dawn and 9:00 A.M. and from 6:00 P.M. to darkness.

Since it was not possible to look into the inaccessible nests, it was especially important to keep them under frequent observation in order to determine any change in rhythm of the nesting visits. In this manner a good approximation of the dates of egg laying and hatching could be made. It was felt that the observation periods were of such regularity that determination of these dates is accurate to within 24 hours. Unless otherwise stated, the figures given for the frequency of the attentive and inattentive periods of the parent at the nest during the various nesting phases are included only if the period of observation exceeded three hours. A nest visit implies complete entry into the nest, except on those occasions during advanced feeding when the female fed the nestling without entering the nest.

The average monthly maximum and minimum temperatures at Simla for Jan., Feb. and

March, 1955, were 61-89, 66-88 and 66-88° F. respectively. The total monthly rainfall for the same months was: Jan., 2.20; Feb., 2.29; March, 2.68 inches.

I am especially grateful to Dr. William Beebe for his many helpful suggestions during this study as well as for placing his highly informative notes at my disposal. I also wish to thank Miss Rosemary Kenedy for assisting me so generously in the photographic phases of this work. Dr. Edward J. Alexander of the New York Botanical Garden kindly identified the nesting material.

THE NESTS

Twenty-three nests were begun at colony A (Plate I, Fig. 1), of which 11 were completed, and at colony B, 14 nests were begun, all of which were completed. The nests at colony A were fairly evenly distributed throughout the tree, whereas at colony B they were bunched together on one side of the tree. Incidentally, at another colony of Crested Oropéndolas, found on March 14 in an adjacent valley at an elevation of about 1,500 feet, the nests were suspended in an immortelle tree some 50 feet above the ground and were all arranged very closely together for a horizontal distance of only about 20-25 feet. Eighteen nests appeared to have been started, of which 14 seemed complete. During a half hour's watch feeding of the nestlings was observed at four separate nests.

High winds apparently take a considerable toll of nests. Four nests (three occupied and one unoccupied) at colony B, and one unoccupied nest at colony A, fell during heavy winds. Two of these fallen nests seemed typical and measurements are given in Table 1.

A great increase in the length of the nest opening and the dispersal of the leaf lining is apparent between incubation and the third week of feeding. Another unoccupied nest, obviously abnormal, measured seven feet in length and weighed 312 grams.

Examination of these nests showed that they were composed largely of the stripped leaf fibers of bromeliads (Bromeliaceae) and heliconia (Musaceae) and stems of vines (Cucurbitaceae). The leaves used in lining the bottom of the nests on the inside were almost exclusively those of the immortelle (*Erythrina micropteryx*). According to Goeldi (1897, 1903) the Crested Oropéndola from southern Brazil employs the fibers of the bromeliad *Tillandsia usneoides* almost entirely as a nesting material, whereas near the Amazon, orchid roots and elongated roots of the rhizomorph *Marasimius* sp. are used. Young (1929) describes a nest

TABLE 1. MEASUREMENTS OF TWO NESTS OF *Psarocolius decumanus*, IN INCUBATING AND FEEDING NESTING STAGES

Nesting phase	Length	Width	Length of opening	Weight (gms.)		
				Fiber	Leaf lining	Total
Incubating	2'10"	8"	5"	93.1	87.7	180.8
Feeding	2'11"	9"	1'5"	178.8	4.1	182.9

from British Guiana as made up of narrow strips of cane leaves, plantain bark, cocoanut fiber and vines. He also states that two or three nests are sometimes built by the same female.

The color of some broken egg shells recovered from a fallen nest was a pale bluish-green or, by comparison with Ridgway (1912), Pale Glauous Green.

THE PRE-INCUBATION AND INCUBATION PERIODS

Dr. William Beebe (unpublished notes) noted nest building in the Crested Oropéndola to be under way in the Arima valley as early as Dec. 5 (1952) and Dec. 23 (1953) and as late as March 4 (1950). Belcher & Smooker (1937) reported that in Trinidad and Tobago nest building began in December and eggs were found from mid-January onwards, with May 24 as the latest date.

The nesting colonies near Simla were not discovered until Jan. 9, 1955, at colony B and Jan. 11 at colony A, at which time nest building was well advanced at both sites. There had been no activity at either tree in late December, 1954, and nest building therefore must have begun either in late December or early January and lasted about two weeks.

Sixteen of the 23 nests started at colony A were being actively worked on during the observation period on Jan. 12. On the following day, however, with 12 nests still incomplete, only two nests were visited by the birds during almost eight and one-half hours of observation. Although most of the nests were no longer actively visited after Jan. 12, there was considerable activity in the nest tree between Jan. 13 and Jan. 18. Periodically small groups made up mainly of females, many of which carried nesting material, would fly into the top of the tree. Here they would remain for varying periods of time, clucking noisily, but with only a few exceptions they made no further attempts at nest building.

Of the 16 nests being built on Jan. 12, only eight were observed to be revisited for the purpose of nest building on subsequent days; one was visited once, two were visited twice, one was visited five times and one was visited six

times, and at only three were visits continued to egg laying and incubation. These last three nests (1, 2 and 3) showed no similarity in the length of time between the end of nest-building and the start of incubation. This pre-incubation activity is summarized in Table 2.

The earliest onset of incubation took place at nest 1 on Jan. 20. In all probability, this nest was completed prior to Jan. 12. Nest 2, however, was not completed until Jan. 14, and incubation did not begin until Feb. 5. Nest 3 appeared to be complete on Jan. 12, with incubation commencing on Feb. 6.

Just why colony A was seemingly abandoned is difficult to explain, for it appeared to be thriving. The observation post was well camouflaged with canvas and concealed by vegetation, in addition to being situated some 100 feet from the nest tree. Moreover, these birds are not particularly known for their shyness, and active colonies are to be found in well-populated areas. In fact, colony B flourished despite its proximity to a rock quarry where frequent blasting was taking place. Dr. Beebe has noted that in the previous three years, as well as the following year (1956), this site always contained medium-sized colonies.

As can be seen by Table 2, nests 2 and 3 were visited frequently and fairly regularly before incubation. It appeared that incubation was under way at nest 3 on the afternoon of Jan. 20, as the female remained in her nest for periods ranging from 23 to 112 minutes during three and a half hours of observation. However, from Jan. 21 to 30 no further activity was noted at nest 3. With this one exception, the length of time spent in the nests at each visit was usually less than a minute, and exceeded five minutes on only three occasions.

Oftentimes, nests 2 and 3 were visited in seemingly unaccountable spurts over relatively short periods of time. The most outstanding example of this behavior took place at nest 2 on the morning of Jan. 29 where, within a period of 44 minutes, the nest was visited briefly 22 times.

The significance of this pre-incubation activity

TABLE 2. PRE-INCUBATION ACTIVITY BY THE FEMALE PARENTS AT COLONY A

Date	Total observation time (min.)	Number of visits per hour			Average time in nest (min.)		
		Nest 1	Nest 2	Nest 3	Nest 1	Nest 2	Nest 3
Jan.							
12	173	0.6	0.3	1.3	<1.0	<1.0	<1.0
13	501	0	0.1	0	0	<1.0	0
14	540	0	0.4	0	0	<1.0	0
15	575	0	0	0.1	0	0	<1.0
16	285	0	0	0	0	0	0
17	410	0.8	0	1.1	<1.0	0	<1.0
18	444	0.9	2.0	1.8	3.7	1.3	<1.0
19	240	0.7	2.7	0.8	<1.0	2.0	9.0
20	210	*	1.1	1.1	*	0.8	58.6
21	180		0	0.6		0	<1.0
22	350		4.1	0		3.1	0
23	245		1.7	0		1.3	0
24	370		0	0		0	0
25	215		2.0	0		2.3	0
26	226		0.5	0		<1.0	0
27	361		4.1	0.1		4.5	<1.0
28	131		3.2	0.4		6.0	<1.0
29	131		11.9	0.9		0.8	<1.0
30	190		2.0	1.2		6.7	4.7
31	352		1.7	0.8		4.4	<1.0
Feb.							
1	170		0.3	0.3		20.0	<1.0
2	350		0.6	1.3		7.5	<1.0
3	80		0	0		0	0
4	83		0.7	2.4		<1.0	<1.0
5	341		*	0		*	0
6				*			*

*Onset of incubation.

is not clear. Since nests 1, 2 and 3 were complete by Jan. 14, after which no nesting material was brought to the nests, and no nest weaving detected, these facts appear to eliminate the possibility that the hens involved were giving "finishing touches" to their nests. Activity ranged from the apparent pseudo-incubation behavior at nest 3 on Jan. 20 to the extremely frequent nesting visits at nest 2 on Jan. 29.

The beginning of incubation was determined by observing the increase in the duration of the attentive periods by the female at her nest. In colony A, the laying of the first egg at nest 1 occurred on Jan. 20, at nest 2 on Feb. 5 and at nest 3 on Feb. 7. The incubation period at all three nests lasted approximately 15 days. During this time the average time spent on the eggs was 74.6% at nest 1, 72.0% at nest 2 and 67.9% at nest 3. The frequency and duration of the attentive periods are indicated in Table 3 and Text-figures 1-3. The percentage of time spent in the nest was determined by dividing the average length of the attentive periods by the sum of the average attentive periods and

multiplying by 100. The number of visits per hour at all nests ranged from 0.5 to 1.9, averaging 1.0 at nests 1 and 3 and 0.8 at nest 2.

For at least seven days prior to egg laying, the female parents at nests 2 and 3 were seen to return to their empty nests at the onset of darkness, and presumably spent the night there. The times of these final entries, as well as those noted during incubation proper, varied from about 5:55 to 6:20 P.M.

THE NESTLING PERIOD

With the sudden increase in the number of nest visits per hour, the hatching of the first egg was considered to have taken place. This occurred at nest 1 on Feb. 4, at nest 2 on Feb. 21 and at nest 3 on Feb. 22. As with incubation, all parental care was undertaken by the females.

The length of nestling life varied from 31 to 32 days at nest 1 and 34 or 35 days at nest 2 to 36 days at nest 3. The amount of time that the hen spent in the nest with the newly-hatched young decreased gradually to less than about 20%. We can refer to this as the brooding

period. At nest 1 this brooding period lasted for seven days, at nest 2 for 11 days and nest 3 for nine days. After the last day of brooding the frequency of visits ranged from 3.2 to 8.5 per hour, averaging 5.7, 5.6 and 5.9 at nests 1, 2 and 3 respectively. Time spent at the nest was usually less than 5% at nests 2 and 3 during the post-brooding period, the length of the average visit being but a few seconds. At nest 1, however, it varied from 5% to 15%, a factor which might possibly have been due to the presence of more than one nestling.

After the cessation of brooding, the females stayed with their nestlings all night for a varying number of days. At nest 1, this period extended for 11 days after hatching, or 34% of the nestling stage; at nest 2 for 26 days (74%), and at nest 3 for 23 days (63%).

The exact nature of the food brought to the netslings could not be determined; however, large orthopterous insects or lepidopterous larvae were frequently noted. Excrement packets were periodically removed from the nests.

By the 18th or 19th day of feeding, the whining of the nestlings, as well as their movements within the nests, could be detected. The young birds are either able to see through the nest wall, or can hear the wing sound of the approaching parent, as often this whining began even before the hen had reached the nest. It usually continued on through the feeding and for a few minutes after she had left. The male can also bring about this whining, for on one occasion a male flying to a branch near an occupied nest caused the young to whine. This, incidentally, induced the male to explore the nest curiously, but he did not enter.

During the early days of feeding the hen entered the nest entirely. But as the nest opening became enlarged by her frequent passage and the nestling increased in size, she fed it either while perching at the nest entrance (Plate I, Fig. 2), or while clinging to the side of the nest.

In the last days of nestling life, the young bird at nest 3 was sometimes seen to climb entirely out of the nest. Then, while clinging to the side and flapping its wings, it would at times completely circle the nest before re-entering.

Nest-leaving took place at nest 1 sometime between 11:30 A.M. on March 7 and 3:30 P.M. on March 8 (31 or 32 days after hatching), at nest 2 between 3:49 P.M. on March 27 and 8:09 A.M. on March 28 (34 or 35 days after hatching) and at nest 3 at 9:07 A.M. on March 29 (36 days after hatching). The following notes were taken on the morning of nest-leaving at nest 3:

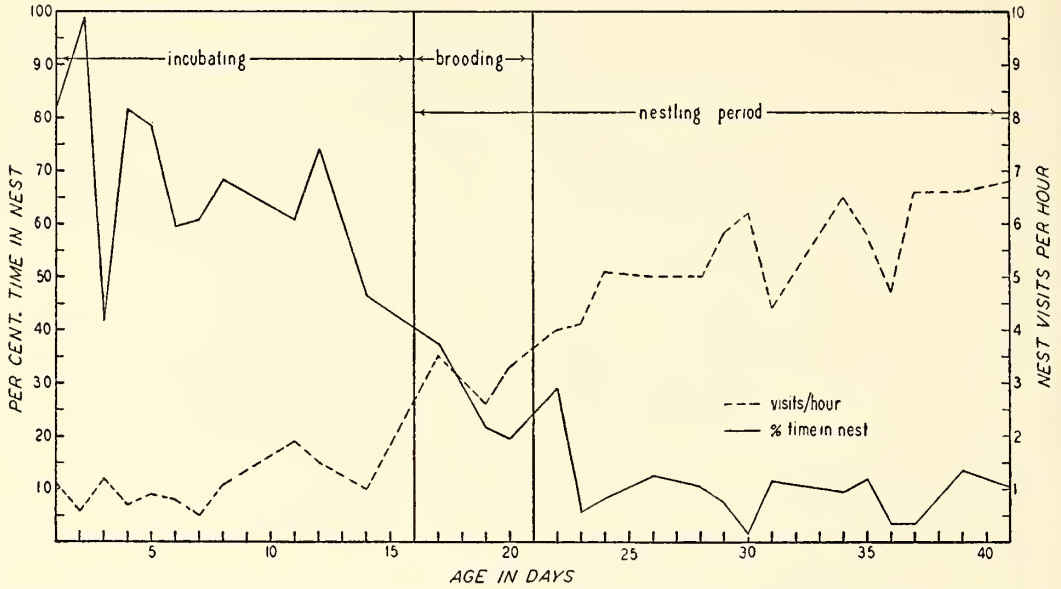
- 7:49 A.M. Observer entered blind.
- 7:50-8:53 Nestling fed on 5 separate occasions.
- 9:02 Nestling had head out of the nest opening before hen reached nest; after being fed it climbed completely out of the nest, perching at the entrance and peering about for a few minutes before re-entering.
- 9:07 After being fed, the nestling perched at the nest entrance for a few seconds, then exercised its wings momentarily and flew off in a fairly strong, slightly descending flight, alighting in a tree some 75 feet away.
- 9:08 Fledgling whined and vibrated wings while being fed.

TABLE 3. PER CENT. OF TIME SPENT IN THEIR NESTS BY THE FEMALE PARENTS AT COLONY A DURING THE INCUBATION AND BROODING PERIODS

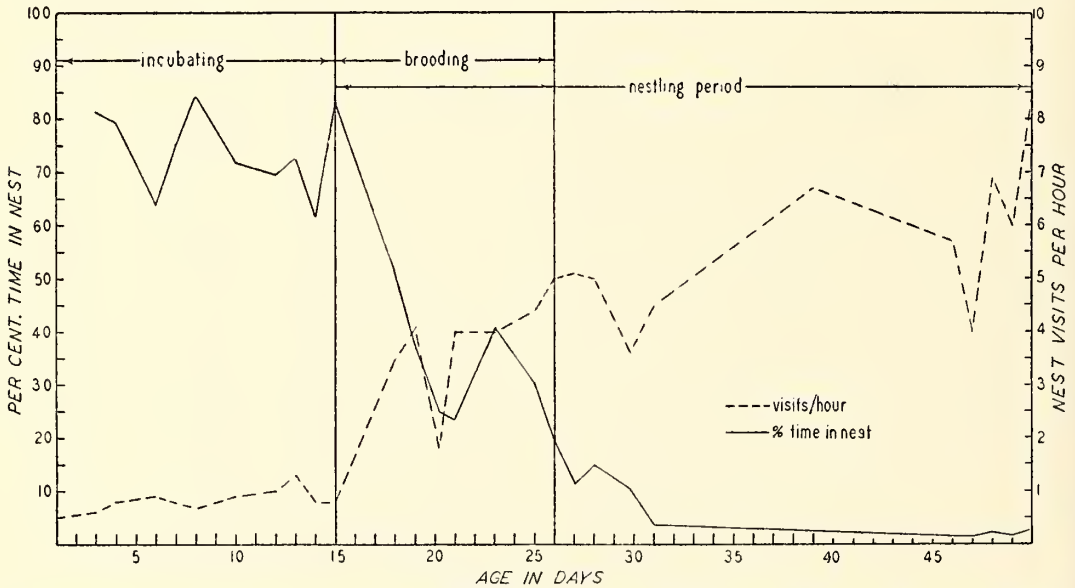
Number of days after egg laying	Nest 1 Jan. 20*	Nest 2 Feb. 5*	Nest 3 Feb. 7*
Incubation			
1	81.8	—	81.0
2	98.8	—	71.8
3	41.6	81.3	—
4	81.6	79.8	73.0
5	78.1	—	58.5
6	59.4	63.9	66.1
7	60.7	75.1	—
8	68.1	84.5	75.4
10	60.9	—	73.9
11	60.9	—	71.2
12	74.0	69.5	65.1
13	—	72.9	85.0
14	42.6	61.5	—
15	—	83.2	72.0
Brooding			
16	—	56.0	—
17	31.9	27.1	59.0
18	—	52.3	23.0
19	22.8	38.3	34.1
20	21.5	44.3	34.5
21	—	25.0	—
22	31.6†	—	24.7
23	—	42.1	28.4
24	—	—	23.7†
25	—	32.4	—
26	—	22.1†	—

*Probable dates of egg laying.

†Last day brooding observed. Percentages not included if observation period was less than 3 hours.



TEXT-FIG. 1. Frequency of nest visits and duration of attentiveness by female parent at nest 1 in colony A.



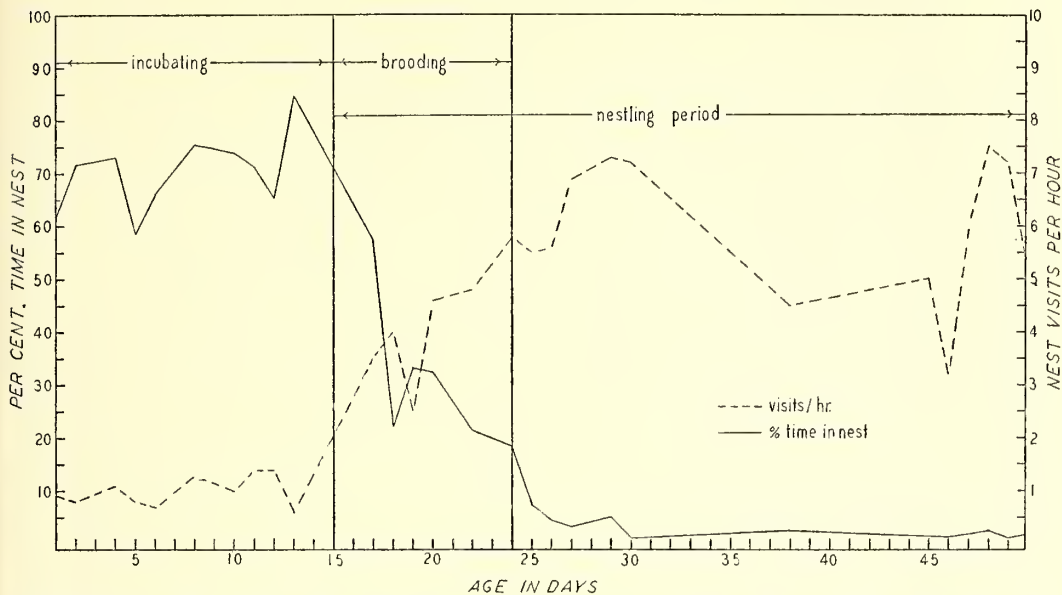
TEXT-FIG. 2. Frequency of nest visits and duration of attentiveness by female parent at nest 2 in colony A.

- 9:09 Fledgling flew to another perch about 25 feet away where it remained perching quietly.
- 9:25 Fledgling fed by hen.
- 9:30 Fledgling flew to another tree about 50 feet distant, again remaining quiet after landing.
- 9:43 Fledgling flew off again; no longer observable.

No more than one nestling was seen at any of the nests at colony A.

VOCALIZATION AND DISPLAY

At first hearing, any description of the various calls of the male Crested Oropendola appears hopeless, as there does not seem to be any particular pattern to his polyphonic and diverse utterances. However, after prolonged and careful listening, they were recognized as falling into four groups:



TEXT-FIG. 3. Frequency of nest visits and duration of attentiveness by female parent at nest 3 in colony A.

CALL 1. An introductory *whaaa cheeee* with the second phrase higher and followed by a continuous, unmusical trill:

whaaa
cheeee

notes usually repeated five times on the same level:

ko ko ko ko ko

CALL 2. Introduction a rising unmusical trill (*rrrrrrrrrup*) followed by *cheow* *wow*, *eow woo woo* or *cheeeeow*, not unlike the meow of a cat:

cheow wow

CALL 3. An introductory *cheeee* (falling in pitch), or a rising *brrrrrree*, *cheeeeow* or *rrrrrrrrrup*, usually diminishing in intensity, followed by *lob lob baah* or *ko ko plo*, repeated three or more commonly four times; the first two notes are given rapidly and the last is drawn out:

ko ko plo ko ko plo ko ko plo

CALL 4. An introductory *peeeeow* or *cheeee* (falling) or *rrrrrrrup* (rising), diminishing in intensity, followed by a series of *ko*, *plo* or *kok*

The most common was Call 1 which comprised 45% of all of those heard. Call 2 was given 24% of the time, Call 3, 16%, and Call 4, 15%.

On numerous occasions the male was heard to utter a confusion of stuttering, gurgling notes, containing some of the elements of a typical display call but wholly lacking in pattern: *oooouuuuuu whup whaaaat upka brrrrrr woo woe whup wheet brrrreew woo*, etc. This was accompanied by much gurgling, feather rustling and wing flapping. It was almost as though a young male were attempting to imitate the call of an adult and failing badly. Every once in a while a male would rather half-heartedly begin a display, but never really finish. Both the abortive gurgling and the unfinished calls were heard during all nesting periods.

Calls 1, 2 and 3 usually accompanied a display, whereas Call 4 was apparently given in the absence of any display.

The male was seen to go through his complete display not only in the presence of females, but also when alone or in the company of males. Dr. Beebe observed two males simultaneously going through a complete display while facing each other. They were some distance from the nest

tree, and no females were noted in the vicinity.

In the typical display, the bird begins by bending forward in a deep bow until his head is well below the perch. At the same time he ruffles his body feathers and brings the extended wings together over the back. The wings are then vibrated rapidly with the primaries open. Almost immediately after the wings are extended, the tail is brought forward quickly over the back until it makes an approximate 90° angle with the back (Plate II, Figs. 1 & 2), and remains in this position from 1.5 to 1.9 seconds. Then, as the tail begins to lower to its normal position, the wing beats become less rapid and take on a flapping or fanning quality which lasts from 1.1 to 2.6 seconds. Sometimes, however, the wing beat does not slacken until the tail has been completely lowered. Finally, the wing flapping stops and the bird comes out of his bow, the entire performance lasting about four to five seconds. These times are based on the analysis of moving pictures taken of five complete displays. The average duration of the four main phases of the display are as follows:

1. Tail elevated forward over back. 0.20 seconds
2. Wings brought together over back and vibrated. 1.74 seconds
3. Tail lowered to normal position. 0.36 seconds
4. Wing fanning or flapping 1.97 seconds

The intervals between beats in the wing-fanning phase were measured at 0.03 seconds. Although not actually measured, many of the display calls seemed to last around five to seven seconds. In all probability, the figures above would have averaged higher if more displays had been analyzed.

Although the spreading of the tail feathers was not noted in the present study, Young (1929) reported it in *Psarocolius decumanus* from British Guinea. This tail spreading during the display is probably characteristic of all oropéndolas, as Fuertes (1916) observed it for the Montezuma Oropéndola and Chapman (1928) for the Wagler Oropéndola.

Displays were frequently performed on the nests proper. In this type of display, the male flew directly to the nest and, clinging to its side, began the display almost immediately upon alighting. The head was always directed downward. In such a position only the initial bowing of the perching display was, of necessity, omitted. Twenty-eight per cent. of all displays at the nest tree were of this type. Crandall (1914) also described this type of nest display for the Montezuma Oropéndola in Costa Rica.

During the 303 hours of observation at colony

A, 683 displays were counted either at the nest tree or from the immediately surrounding trees. The displays from the nest tree numbered 320, and those from the nearby trees, 363. The frequency of displays given on or near the nest tree ranged from 0.1 to 10.2 per hour, with an average of 2.2 per hour throughout all nesting periods. At no time of the day was the display observed to be given more frequently.

Often a male would fly to a nest and perform no display. On the other hand, there were instances where a male displayed on as many as five different nests in succession. There seemed to be no particular preference in selecting the nests to display on, and oftentimes an occupied nest was flown to while a hen was incubating, whereupon she would usually vigorously chase the male just as she would a cowbird. Sometimes when a group of males were in the nest tree and one of them flew to a nest, another male would chase it off and, as though stimulated by this chase, then go through a complete nest display. On one occasion this type of behavior was repeated three times in the course of about three minutes by the same pair in the same respective roles. It was a fairly common practice for males accompanying returning females to the nesting colony to display almost as soon as they arrived in the nest tree.

The most common note of the female was a *cluck* which she sometimes uttered repeatedly for considerable periods of time while perching, preening or flying about the nest tree. Often, when she first came to the nest tree after an inattentive period, during either incubation or feeding, she clucked continuously sometimes up to 15 minutes before finally entering her nest. Less frequently she carried on this clucking after leaving the nest. When annoyed or disturbed, the clucking became more rapid. Although not noted for certain, the male probably also gives a similar *cluck* note. Skutch (1953) reports this in the male Montezuma Oropéndola. In chasing cowbirds, males or other females from her nest or its vicinity, the hen generally voiced a harsh, nasal mewling rising at times to a high-pitched whine.

As is characteristic of all oropéndolas and caciques, a warning *cack* is given by the male at the approach of danger. This seemed to be most often brought on either by the sight or scream of the Gray Hawk (*Buteo nitidis*), or the sudden appearance of man. Frequently after the sounding of an alarm *cack*, the oropéndolas present failed to leave the nest tree or its immediate area, and incubating hens rarely left their nests.

COWBIRD ACTIVITY

The visitations of Giant Cowbirds (*Psomo-*

colax oryzivorus) to colony A were carried on with persistent regularity between Jan. 13 and March 4. On the latter date the nestlings were 26 to 43 days old. After March 4 only one further cowbird visit was noted, on March 23. On 34 of the 50 days between these dates, cowbirds were seen coming to the nest tree at one time or other on 52 separate visits. Cowbird activity was recorded on 77% or 29 of the 37 days in which the observation periods lasted longer than three hours.

It was interesting to note that on 34% of their visits, the cowbirds came to the nest tree following returning female oropéndolas. In the majority of cases only one cowbird visited the colony at any one time. However, on five occasions two cowbirds came to the nest tree together, and once a group of four came in together.

Usually the cowbirds immediately began inspecting a series of nests. At colony A most of the nests were unoccupied. The process of the inspecting consisted in momentarily peering into the nest opening, and only on two occasions were cowbirds seen to enter the nests completely. If the nest happened to be occupied by an incubating female, she would always give her scolding whine and usually give immediate chase. The cowbird was chased for only a short distance, after which the female oropéndola would usually immediately return to her nest. Often the same cowbird would return immediately, only to be chased again from the same or other nests. Only three instances were noted when an incubating or brooding female did not leave her nest to chase a cowbird, but instead merely voiced a scolding whine from within. On several occasions cowbirds were chased from unoccupied nests by females who happened to be either returning or leaving their nests. These chases were not especially energetic, however, and pursuit was not vigorous.

Male oropéndolas were rarely seen to chase cowbirds, and when both cowbirds and males were in the nest tree at the same time, neither seemed very disturbed by the other's presence even when perched only a few feet apart. If cowbirds remained quietly in the nest tree they were never observed being chased even by females.

Cowbirds were never noted to remain for very long in the nest tree during inspecting visits. The average length of time was only two to three minutes.

From all indications, cowbirds appeared to have had little success in parasitizing any nests at colony A. Only two nests were ever observed to be entirely entered, and these for but a few seconds.

THE NESTING AT COLONY B

The various nesting phases at both colonies were relatively comparable. On the first day of observation at colony B (Feb. 6) nestlings were present in three nests and incubation was under way in five of the 11 nests eventually occupied. On the same date at colony A, one nest contained young and two were incubating. As shown in Table 4, three of the 14 original nests were never occupied, and of the remaining 11, three fell, leaving eight (73%) of the occupied nests to produce fledged young.

Nest number 3, which the nestlings had left by March 6, was seen to be revisited on March 13. During observation periods in the following three weeks a female was seen to visit it, but the nature of the visits could not be determined with any certainty. This might possibly be an instance of the rearing of a second brood. In 1956 Dr. Beebe noted nest activity by females at colony A as late as June 4, again indicating the possibility of a second brood.

The general activity at colony B was much the same as that at colony A, but naturally on a larger scale. The times of the various nesting phases were similar, with incubation lasting about two weeks and feeding from about four to five weeks.

MISCELLANEOUS OBSERVATIONS

Most of the time the females went about their various activities independently. However, it was not uncommon to see two hens leave or return to their respective nests at the same time. This was observed not only when they left the nests for the first time in the morning and at the final entry at the coming of darkness, but also during regular daytime activity. For ex-

TABLE 4. SUMMARY OF THE NESTING PHASES FOR THE OCCUPIED NESTS AT COLONY B. (I=incubating; N=nestling period; F=nestlings fledged; X=nest fell; R=nest reoccupied).

Nest	February				March				April
	6	13	20	27	6	13	20	27	3
1	—	I	X						
2	N	N	N	X					
3	N	N	N	N	F	R?			
4	N	N	N	N	F				
5	I	I	I	N	N	X			
6	I	I	N	N	N	F			
7	I	I	I	N	N	N	N	F	
8	—	I	I	N	N	N	N	F	
9	—	I	I	N	N	N	N	F	
10	I	I	I	N	N	N	N	N	F
11	I	I	I	N	N	N	N	N	F

ample, on March 4 the three females at colony A, who were feeding their nestlings, either entered or left their nests 218 times during six and a half hours of observation. On 23 (10%) of these nest entries or departures, two females were seen either to leave or arrive at their nests together.

Copulation was seen on but one occasion at the nest tree; this took place in the late afternoon (6:00 P.M.) on Feb. 2. The male approached one of a pair of females and displayed, after which he began to peck at her cloacal area. The female fluttered her wings but otherwise remained fairly still. The male then engaged in a brief copulatory act and followed this by pecking at her cloacal region once more, while she squatted and fluttered her wings again slightly. The male then went through another complete display.

Other than the cowbirds, all species of birds that visited the nest tree at colony A remained unmolested. Once a Gray Hawk (*Buteo nitidis*) flew into the nest tree and perched undisturbed for a few minutes before flying off. It was apparently unseen by the oropéndolas of the colony, as the recognized presence of a hawk in the vicinity would invariably elicit the sounding of the alarm *cack*. Once at colony B, when a Gray Hawk flew overhead, several oropéndolas took off in pursuit.

DISCUSSION AND SUMMARY

The nesting activity of two colonies of the Crested Oropéndola (*Psarocolius decumanus insularis*) in the Northern Range of Trinidad, B.W.I., was studied from the end of nest building to nest leaving by the young. Fourteen nests were completed at one colony all of which were later occupied, and 11 were completed at the other, of which three were occupied. The relative length of the various nesting phases as well as the general activity were similar at both colonies. Nesting success at the colony with the three occupied nests was 100%, and at the colony with the 11 occupied nests, 73%. Nest building and care of the young were undertaken entirely by the females. The following discussion and summary are based on the observations at the colony containing the three occupied nests.

The period from the completion of nest building to the beginning of incubation varied from 7 to 25 days with the incubation period proper lasting 15 or 16 days. This is but slightly longer than the incubation of 11 to 14 days reported in the literature for the family Icteridae. The average time spent on the eggs ranged from 68% to 75%.

The nestling period varied from 31 to 36 days, and brooding from 7 to 11 days. These nestling periods do not vary significantly from those of 30 to 37 days given by Chapman (1928) and Skutch (1954) for two other oropéndolas: *Gymnostinops montezuma* and *Zarhynchus wagleri*. After the cessation of brooding the females remained with the nestlings at night from 11 to 26 days, or 34% to 74% of the nestling period.

The different phases of the male perch display were analyzed with the aid of motion pictures. Comparisons with the descriptions in the literature of the display of other oropéndolas (*Psarocolius decumanus*, Chapman, 1894, Young, 1929; *Gymnostinops montezuma*, Fuertes, 1916, Skutch, 1954; and *Zarhynchus wagleri*, Chapman, 1928) emphasize the marked similarity of the sequence of display phases among oropéndolas. This similarity is brought out in Plate II, which compares the perch displays of the Crested and Green Oropéndola. Displays were frequently performed on the nests proper, and 28% of all displays at the nest tree were of this type. The frequency of all displays given on or near the nest tree averaged 2.2 per hour throughout all nesting periods.

The various calls of the male were analyzed and found to fall into four separable groups. These calls, although of a similar quality to those reported for other oropéndolas (*op. cit.*), appear to differ considerably, not only within the oropéndola complex, but also within the same genus. Beebe (unpublished notes) records *Psarocolius decumanus* from Trinidad as calling wholly unlike *Psarocolius angustifrons* from Venezuela; and Friedman & Smith's (1950) description of the call of *Psarocolius decumanus* from northern Venezuela does not seem to resemble closely any of the calls of the Trinidad birds.

Persistent cowbird activity was noted from the termination of nest building on to advanced feeding, at which time the nestlings were 26 to 43 days old. During this period cowbirds were seen to visit the colony to inspect nests on about 77% of the observation days. This type of persistence by Giant Cowbirds was also noted by Skutch (1954) in a colony of Montezuma Oropéndolas.

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EXPLANATION OF THE PLATES

PLATE I

- FIG. 1. View of colony A from observation blind (February).
- FIG. 2. Female parent feeding nestling in nest 3 at colony A (March).

PLATE II

- FIGS. 1 & 2. Male Crested Oropéndolas (*Psarocolius decumanus*) displaying in nest tree at colony A.
- FIG. 3. Beginning of display in the male Green Oropéndola (*Psarocolius virens*). New York Zoological Park.
- FIG. 4. End of display in the male Green Oropéndola. Note bow is deeper than in *P. decumanus*.



FIG. 1



FIG. 2



FIG. 1



FIG. 2



FIG. 3



FIG. 4



Changes in the Cytological Structure of the Adenohypophysis and Gonads in Juvenile *Bathygobius soporator* after Pituitary Implantation¹

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(Plates I & II)

INTRODUCTION

THE relationship of the pituitary and the gonads has been studied and acknowledged in all vertebrate classes. General seasonal changes in the pituitary and gonads of the goldfish and carp were described by Scruggs (1951) and correlated with the previous literature on the subject in teleosts. No report has been found on the histology of the specific cell types of the pituitary correlated with the histology of the gonads after experimentally induced changes in the two tissues. The present report is a histological study of gonads and transitional lobes of pituitaries of juvenile fish after pituitary implantation.

All fish used were collected in shallow water areas around North Bimini Island, Bahamas, B. W. I. Experimental work was done at the Lerner Marine Laboratory on Bimini.

The help given during this study by Dr. C. M. Breder, Jr., and Miss Priscilla Rasquin is gratefully acknowledged.

MATERIALS AND METHODS

The marine teleost *Bathygobius soporator* (Cuvier & Valenciennes) was used. This species is very hardy and will survive the handling involved during implantation. Since these fish do not engage in active swimming to a large extent, the incision healed rapidly and no stitches were necessary.

Twenty-five young *Bathygobius soporator* of an average standard length of 38 mm. were given intraperitoneal implants of whole pituitary

glands from larger fish of the same species. The average standard length of the donors was 66 mm. All 25 fish received three pituitaries each.

Pituitaries were obtained by the following procedure. The donor fish was heavily anesthetized in ethyl urethane dissolved in sea water. The lower jaw was removed and the floor of the cranium with its covering membranes was cut away with small bone clippers, exposing the pituitary. The area for cutting was determined by the position of the saccus vasculosus, which could be seen through the bone. Pituitaries were removed by grasping the infundibulum with watch-maker forceps and pulling gently. The pituitaries were held in physiological saline (0.6%) until all three were collected.

The recipient fish was lightly anesthetized with ethyl urethane and placed on cotton saturated in sea water. A slit was made in the abdominal wall lateral to the midline with watch-maker forceps and the three pituitaries were introduced through the slit. A dissecting microscope was used while removing and implanting the glands. Immediately after implantation, the fish were placed in individual two-gallon tanks with running sea water.

The gonads of the donor fish were removed and fixed in Bouin's picro-formol solution, embedded in paraffin, sectioned at 10μ , and stained with Harris's haematoxylin and eosin. The fish receiving the implants were killed after varying lengths of time. Eighteen fish were killed at seven to eight days, and seven fish from two and one-half to three days post-operative. Their bodies, minus the heads, were fixed in Bouin's, sectioned at 10μ through the region of the gonads and stained with Harris's haematoxylin and eosin. Heads of the 25 experimental fish were fixed,

¹This study was supported in part by a grant from The National Science Foundation.

embedded in paraffin and sectioned at 5μ . The modification of Halmi's paraldehyde fuchsin stain by Sokol (1953) provided an excellent stain with which to observe the response of any specific cell group of the pituitary to a given experimental procedure. Bouin's fixative and the paraldehyde fuchsin stain were used for the heads of 18 of the experimental fish, and Baker's fixative and acid haematin stain were used for the seven other experimental fish. The paraldehyde fuchsin was used specifically for the study of basophils and the acid haematin for acidophils.

A group of 11 normal fish were killed and prepared for histological study by the same methods used for experimental fish. The normal fish ranged from 80 mm. to 29 mm. in standard length. All stages of normal gonad development and maturation were represented in this series.

Tavolga (1955) reported that *B. saporator* collected in the area of Marineland, Florida, were at the height of the spawning season in July and August. However, the largest gobies which were collected for the present study in Bimini waters were judged by gross dissection and histological section to be in or near spawning condition in March and April. Testes were swollen, nearly white in color and had high epithelium; ovaries were bright yellow and thin walled as described by Vivien (1941) as characteristic of the spawning condition for the European goby, *Gobius paganellus*.

The largest female collected by Tavolga (1954) was 65 mm. in standard length, while males of 90 mm. or more were found. In Bimini, the largest female found was 87 mm. and the largest male 108 mm. The mean, of course, was lower, the average of 43 females being 66 mm. and of 56 males, 74 mm.

Testes of eight normal *Bathygobius* were stained with Sudan Black B and by the Baker technique for phospholipids. The testes of one fish which had received three pituitary implants and maintained for one week was also stained with Sudan Black B.

RESULTS

Implants of pituitaries of mature fish to juvenile fish caused degranulation of the basophils of the adenohypophysis and stimulation of the gonads. The acidophils of the transitional lobe were not affected. In both experimental and control fish, the acidophils were large, well-rounded and heavily stained with the Orange G of the paraldehyde fuchsin stain. The acidophils stained with acid haematin did not show degranulation.

Degranulation of the basophils occurred in nine fish which had received implants and were

maintained for one week before being killed. Little or no degranulation was seen in seven fish sacrificed three days after receiving pituitary implants, nor in two fish maintained for one week before killing. The latter had gonads in very early stages of maturation and it is thought that the tissue may be refractory at this early stage. Partially degranulated basophils of a three-day implant are shown in Plate I, Figure 1, and may be contrasted with the advanced degranulated condition found in a seven-day implant shown in Figure 2. Normal acidophils are shown in Figure 3.

The degranulated basophils are found along the periphery of the pituitary and in groups along the region of juncture with the intermediate lobe. The centers of the cells are clear and the cells somewhat shrunken and collapsed. Dark-staining granular material may be seen between the cells. The basophils of the control and non-reactive experimental fish are large and have either very small clear areas or none. The basophils take a very heavy and dark stain.

Atz (1953) described basophils similarly located in the fresh water teleost, *Astyanax mexicanus*. The correlation of changes in the peripheral basophils with changes in the gonads led her to consider these cells as gonadotrophs. In all but one case basophils were reported to have increased in number near the time of onset of the spawning season. In no case was there a report of degranulation occurring at this time. In the present experiment no increase in the number of basophils was noted.

The possibility of basophilic degranulation occurring as a result of stress and loss of ACTH was considered. However, two fish which survived seven days showed no degranulation and the seven fish which were killed after three days, an even shorter time to adjust to stress, showed little or no degranulation.

The testes of *Bathygobius saporator* have an unusual amount of tissue which is not spermatogenic. The functional germ cell tissue of the testis is spirally wrapped around a core of tissue of very different nature. The core tissue has some resemblance to interstitial tissue but the amount seems out of proportion to the need or to the amount of interstitial tissue found in other teleosts. The intimate relation of the germ cell tissue and the core tissue would indicate that the core is a functional part of the testis but no definite function has been described.

Gonads, especially the ovaries, were stimulated in the fish showing degranulation. The stimulation caused rapid maturation of about half the ova and a third of the spermatogonia but little increase in over-all size of the gonad.

However, the core tissue of the testes hypertrophied. Stimulation was greater when the pituitary donor had gonads in intermediate stages of maturation than when the gonads were very advanced and approaching or in spawning condition. An ovary from an untreated juvenile and an untreated mature fish are shown in Plate I, Figures 4 and 5. Figure 6 shows the response of an ovary to the experimental procedure. The ovary from the mature untreated fish shows more uniform graded development than that of the treated juvenile fish where several ova are highly developed while the rest are in a uniform early stage.

Testicular and core tissue of an untreated juvenile and untreated mature fish are shown in Plate II, Figures 1 and 2. The normal condition of the core tissue of a juvenile fish stained with Sudan Black B to show lipids is shown in Plate II, Figure 3, and is contrasted with Figure 4 of the same magnification which shows the hypertrophied core tissue from a fish which had received pituitary implants. Baker's acid haematin and pyridine extraction techniques were used on the core tissue to indicate some of the cellular components. Staining results of the core tissue of normal fish showed a positive reaction to acid haematin (Plate II, Figure 5) and a negative one to pyridine extraction (Plate II, Figure 6), indicating the presence of phospholipids.

DISCUSSION

The histology of the pituitary and the identification of cell types as sites of specific hormone production is still to some extent controversial. In the teleosts the transitional lobe has been found to be homologous to the anterior lobe in other vertebrates (Charipper, 1937).

The pituitary basophils of the rat were described as the site of thyrotropic and gonadotropic hormone elaboration and storage by Purves & Griesbach (1951). A subsequent report (1954) designated the specific basophils which produce TSH, FSH and LH.

However, there is some disagreement as to whether the gonadotropic hormone is a single biochemical entity or two or even more. Evans & Simpson (1950), in a review of the literature concerning the gonadotropins, called attention to the fact that it is not certain that there are two distinct gonadotropic hormones identical with the two substances which have been isolated from pituitary tissue or that both hormones are necessary in both sexes for normal reproductive function. The gonad maturity at the time of pituitary injection for experimental purposes is an important factor.

Matthews (1939), using injections of mam-

malian pituitary extract on *Fundulus heteroclitus*, found that the injections had no stimulating effect in the males and only four of 35 females responded to any degree. Hypophysectomy caused regression of the gonads especially in the males. On the basis of this work the pituitary gland of a teleost was seen to exert a controlling influence on the seasonal cycle and this influence was considered to be "... of greater importance in maturation than in proliferation of the germ cells." The present study is in agreement, as pituitary implantation caused an acceleration in the rate of maturation of the germ cells.

The effect of adult *Fundulus* pituitary implants to immature fish of the same species was reported by Matthews in 1940. Adult pituitary implanted intraperitoneally into immature fish at three-day intervals caused gonad stimulation by the end of four weeks. The males were especially responsive and large numbers of mature spermatozoa were seen. The pigmentation of the fish was characteristic of the adult in breeding season. Included in this report was a review of the use of mammalian pituitary extracts for injection in fish and the conflicting results and data collected; in many cases the mammalian preparation had no effect. A similar review of the use of injecting fish pituitary preparations in fish showed a fairly uniform response. All species tried showed enlargement of the gonads and in some cases expulsion of eggs and sperm. All experiments involving hypophysectomy showed gonad regression.

Burger (1941) used pituitaries from adult *Fundulus* as implants to other adult male *Fundulus* which had been hypophysectomized at the time of maximal testicular development and which showed inhibition of the testes after hypophysectomy. The implants caused recrudescence of the testes within two weeks. The implants were made intraperitoneally and each fish received five at a time for four times. Burger concluded that the *Fundulus* pituitary contained gonadotropic material which was responsible for spermatogonial proliferation and for the maturation phenomena.

Riley & Fraps (1942) investigated the gonad-stimulating activity of anterior pituitary in the female domestic fowl. Glands from hens with regressed or quiescent ovaries produced a greater stimulation of the gonads in immature mice than glands from hens in full reproductive condition. Greater gonad stimulation of the gobies in the present report resulted when pituitary donors were in intermediate stages of gonadal development.

The cyclic changes in the pituitary of the urodele amphibian (*Taricha torosa*) were described by Miller & Robbins (1955). In this form the

delta basophils of the pituitary increase in number and granulation in relation to spring spermatogenesis and oogenesis and late fall final gonad maturation. The beta basophils were considered to be related to increased thyroid activity.

As part of a study of light and temperature effect on the sexual cycle of the bitterling *Rhodeus amarus*, Verhoeven & van Oordt (1955) studied the adenohypophysis of the fishes which had an experimentally induced sexual cycle. They briefly note that the beta cells of the gonadotropic zone had become more numerous and staining response of these cells to PAS was a deep purple coloration which in rats indicates gonadotropic hormone. The method by which an increase in the number of beta cells was ascertained was not given.

Rasquin & Stoll (1955) described the association of degranulated centrally located basophils with hypertrophied adrenals in the freshwater teleost *Astyanax mexicanus* after injections of pitressin. The degranulation was thought to be a result of loss of ACTH, as the thyroid tissue was not stimulated. The peripheral basophils (suspected of gonadotropin elaboration) did not degranulate.

The only possible explanation for the appearance of degranulated basophils after pituitary implantation in the present study is that the basophils are not elaborating secretion granules at the normal rate because of the excess pituitary substance which was added. The absence of granules in cells usually crowded with them is generally interpreted as a release of hormone, but since the fish were given more pituitary there would appear to be no need for the pituitary of the implanted animal to add its secretion to a system already over-supplied. The fact that the degranulation was so gradual—little or none could be detected after three days of implantation—supports the idea that degranulation in this case is a result of an inhibition of elaboration rather than a stimulated release of secretory products which would presumably occur more rapidly.

Sections of the core tissue of testes of *Gobius auratus* Risso were stained and found to be faintly fuchsinophilic and unblackened by iron haematoxylin (Eggert, 1931). The granules within the cells of the tissue apparently contained lipids. Included in the report is a survey of the literature on the core tissue and a discussion of the possibility that this is the interstitial tissue. Eggert claimed that the fine vacuolation and granulation indicated that the cells were not interrenal. He did not find core tissue in the testes of *G. panizae* Verga, *G. buchichi* Steindachner, *G. quagga* Heck or *G. jazo* Linnaeus.

Coujard (1941) described the core tissue in *Gobius niger* and *G. minutus* as being made up of cells with large nuclei and nucleoli, abundant in protein and containing lipids. He did not attribute a definite function to the tissue but considered that it undoubtedly had a function correlated with glandular development and the nervous mechanism of spawning.

The procedure for demonstrating phospholipids has been described in detail by Baker (1946). He used the two-stage technique of acid haematin staining and pyridine extraction on several tissues, including the testes of the mouse. The secretion droplets of the interstitial cells reacted positively to acid haematin and negatively to pyridine extraction, which identified the secretory granules as phospholipid.

Melampy & Cavoza (1954) made a comparative study of lipids in the vertebrate testis, using Sudan dyes and Baker's acid haematin-pyridine extraction technique. Using the Sudan dyes, a positive reaction was obtained from the interstitial cell cytoplasm, basement membrane, cytoplasm of Sertoli cells, spermatogonia, spermatocytes and spermatids of the bull, ram, boar, guinea pig, rooster and horned lizard. The teleost, the bluegill (*Lepomis macrochirus*), showed a negative reaction with the Sudan dyes. The authors suggest that the failure to get a positive reaction from bluegill testis might be due to the cyclic breeding season of this form and that at the stage of the test the reactive quantity of cholesterol in the testis was absent. Baker's test was not applied to the bluegill testis.

The implantation experiments reported here show that the core tissue of the testis is responsive to pituitary stimulation. The marked hypertrophy of the cells, the high phospholipid content and the close proximity of the core tissue to the spermatogenic cells seem sufficient evidence for designating the core cells as interstitial tissue.

SUMMARY

1. Pituitary implants from adult fish to juvenile fish caused degranulation of the peripheral basophils of the transitional lobe of the hypophysis and gonad stimulation in receiver fish maintained for one week after implantation.

2. Basophils of fish maintained for three days after implantation showed little or no degranulation.

3. Acidophils of the adenohypophysis were not affected by the experimental procedure.

4. Degranulation which occurred gradually may be the result of inhibition of hormone elaboration rather than stimulation of release of hormone.

5. Basophilic degranulation, when it occurred,

was the same in both sexes but acceleration of maturation of the ovary was greater than that in the testis.

6. The core tissue of the testes hypertrophied after pituitary implantation and had a high phospholipid content. On this evidence, the core tissue is designated as interstitial tissue.

7. The degree of gonad maturity of the pituitary donors was an important factor in the results. Greater stimulation resulted when donors were in intermediate maturation stages than when donors were in advanced stages.

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EXPLANATION OF THE PLATES

PLATE I

- FIG. 1. Partially degranulated basophils in a 41 mm. fish three days after pituitary implantation. Paraldehyde fuchsin, sagittal section, 1500 \times .
- FIG. 2. Peripherally located degranulated basophils from a 40 mm. fish killed one week after pituitary implantation. Paraldehyde fuchsin, sagittal section, 1500 \times .
- FIG. 3. Normal acidophils and basophils from 43 mm. control fish, paraldehyde fuchsin, sagittal section, 1500 \times .
- FIG. 4. Ovary of 55 mm. untreated juvenile. Haematoxylin and eosin, cross section, 100 \times .
- FIG. 5. Ovary of 73 mm. untreated adult. Haematoxylin and eosin, cross section, 100 \times .
- FIG. 6. Stimulated ovary from 42 mm. fish after one week of pituitary implantation. Haematoxylin and eosin, cross section, 100 \times .

PLATE II

- FIG. 1. Core and spermatogenic tissue of 41 mm. untreated juvenile. Haematoxylin and eosin, cross section, 100 \times .
- FIG. 2. Core and spermatogenic tissue of 80 mm. untreated adult. Haematoxylin and eosin, cross section, 100 \times .
- FIG. 3. Core tissue of 41 mm. untreated juvenile stained with Sudan Black B, cross section, 500 \times .
- FIG. 4. Core tissue of 35 mm. juvenile after one week of implantation. Sudan Black B, cross section, 500 \times .
- FIG. 5. Core tissue of 81 mm. adult stained with acid haematin, cross section, 1500 \times .
- FIG. 6. Core tissue of 74 mm. adult after pyridine extraction, cross section, 1500 \times .

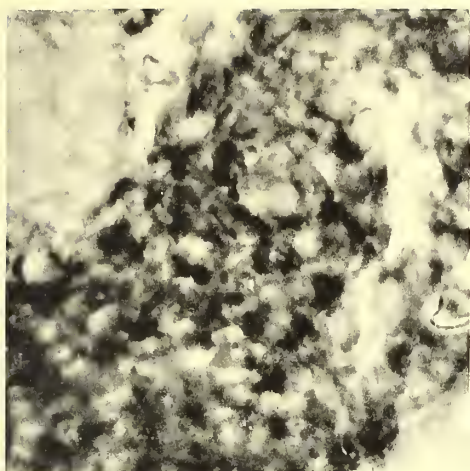


FIG. 1

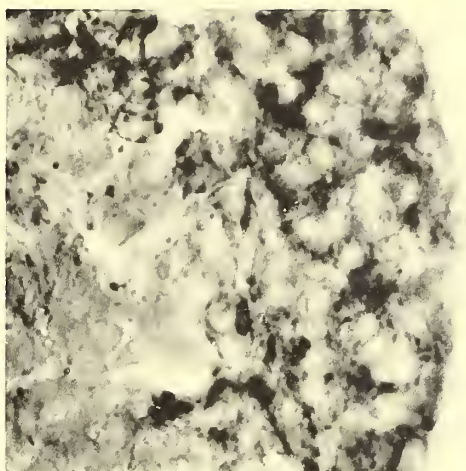


FIG. 2

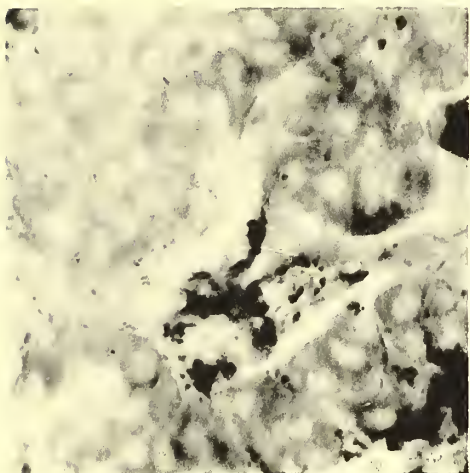


FIG. 3



FIG. 4

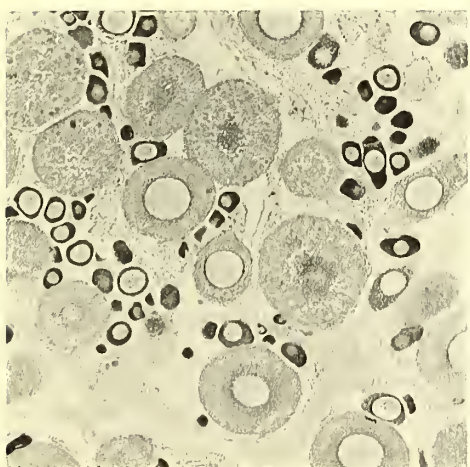


FIG. 5

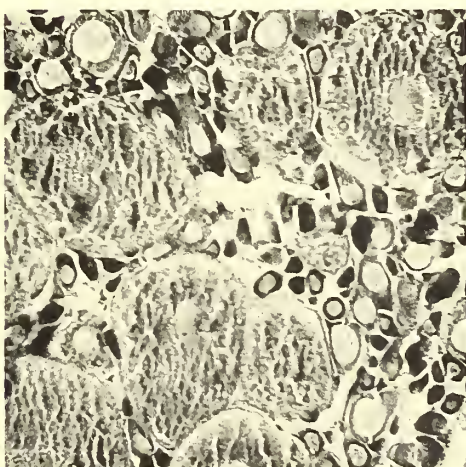


FIG. 6

CHANGES IN THE CYTOLOGICAL STRUCTURE OF THE ADENOHYPOPHYSIS AND GONADS IN JUVENILE BATHYGobiUS SOPORATOR AFTER PITUITARY IMPLANTATION



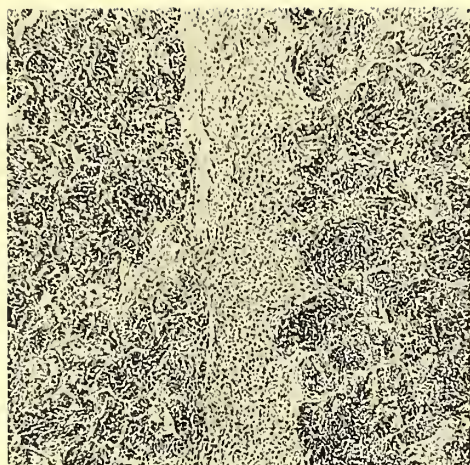


FIG. 1

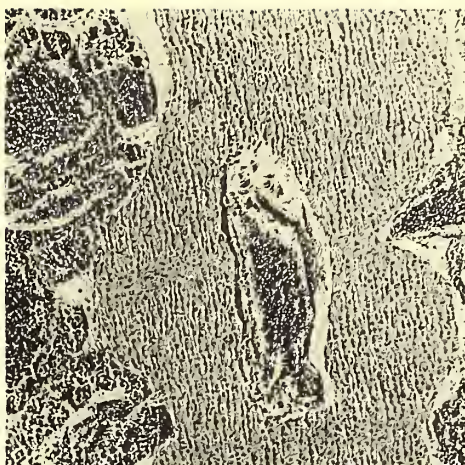


FIG. 2

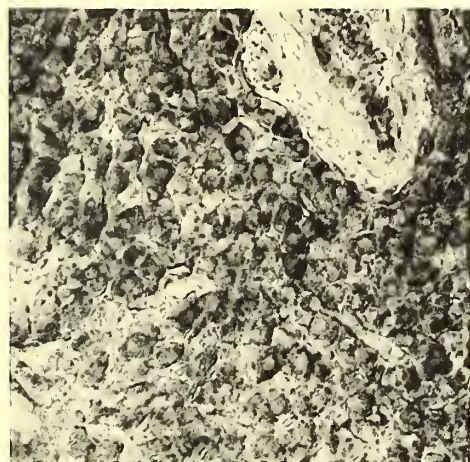


FIG. 3

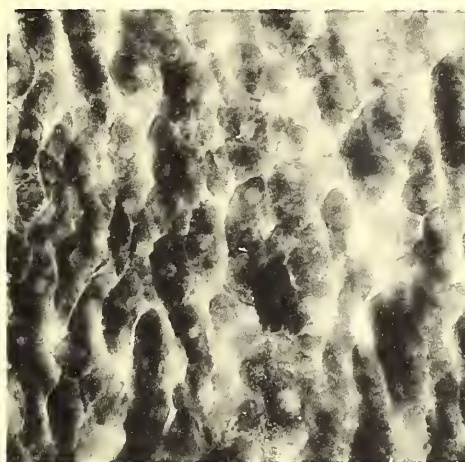


FIG. 4

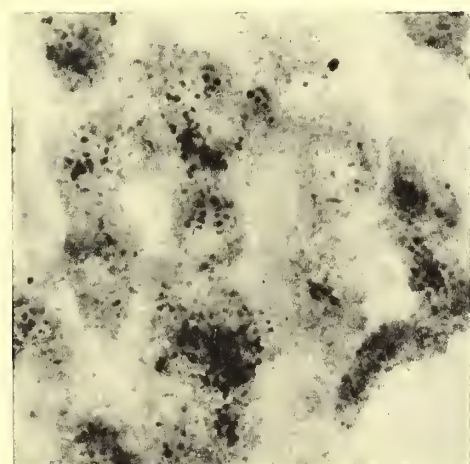


FIG. 5

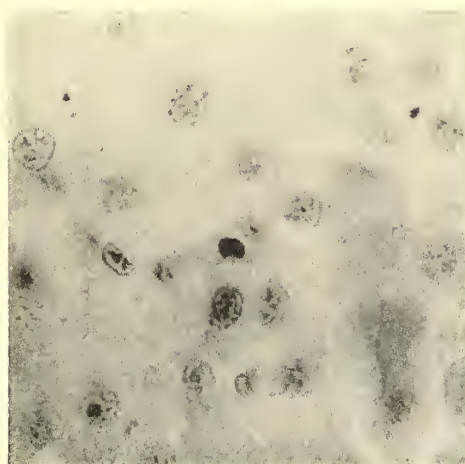


FIG. 6

CHANGES IN THE CYTOLOGICAL STRUCTURE OF THE ADENOHIPOPHYSIS AND GONADS IN JUVENILE
BATHYGOBIUS SOPORATOR AFTER PITUITARY IMPLANTATION

The Ctenuchidae (Moths) of Trinidad, B. W. I.

Part I. Euchromiinae.¹

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(Plates I-III)

[This paper is one of a series emanating from the tropical Field Station of the New York Zoological Society, at Simla, Arima Valley, Trinidad, British West Indies. This station was founded in 1950 by the Zoological Society's Department of Tropical Research, under the direction of Dr. William Beebe. It comprises 200 acres in the middle of the Northern Range, which includes large stretches of undisturbed government forest reserves. The laboratory of the station is intended for research in tropical ecology and in animal behavior. The altitude of the research area is 500 to 1,800 feet, with an annual rainfall of more than 100 inches.

[For further ecological details of meteorology and biotic zones see "Introduction to the Ecology of the Arima Valley, Trinidad, B.W.I.," William Beebe. (Zoologica, 1952, Vol. 37, No. 13, pp. 157-184).]

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INTRODUCTION

THIS paper concerns the species of moths belonging to the subfamily Euchromiinae that have been reported in the literature or collected by the Department of Tropical Research of the New York Zoological Society at its biological station at Simla, Arima Valley, Trinidad, B.W.I. The subfamily Ctenuchinae will be treated in a subsequent paper which will also include keys to all the genera of Ctenuchidae found in Trinidad, as well as the bibliography.

I have followed Travassos (1935: 437-451) in the selection of the family name for this group of moths. Ctenuchidae has priority over other names in use as follows:

Ctenuchidae, Kirby, 1837.

Syntomidae, Snellen, 1867.

Euchromiidae, Neumoegen & Dyar, 1893.

Amatidae, Jansen, 1917.

While the type genus of Syntomidae, *Syntomis*, has been found to be a junior synonym of *Amata*, the emendation of the XIVth International Congress of Zoology at Copenhagen, 1953, states that a family group taxon based on a synonymized genus is not to be changed (Copenhagen Decisions on Zoological Nomenclature: 36, par. 54 (1) (a), 1953). The Syntominiinae are limited to the Old World and do not concern us in this paper.

¹Contribution No. 978, Department of Tropical Research, New York Zoological Society.

No attempt has been made to make the references under the species complete. References to the original description, pertinent or new synonymy, colored figures, helpful descriptions to the species or a specific reference to Trinidad have been cited, however.

Three publications cited whenever possible are:

Hampson, G. F.: Catalogue of the Lepidoptera Phalaenae, I, Syntomidae, 1898; Supplement I, Amatidae, 1914.

Seitz, A.: Macrolepidoptera of the World, VI, Euchromiidae, 1915 and 1917.

Kaye, W. J. & N. Lamont: A Catalogue of the Trinidad Lepidoptera Heterocera. Mem. Dept. Agric. Trinidad and Tobago, No. 3, 1927.

This paper includes keys to the species of moths found in Trinidad and photographs of the species collected at Simla, Arima Valley, in an attempt to make it useful to biologists working on ctenuchids in Trinidad. Five new species of Euchromiinae are described.

The species of Ctenuchidae of Trinidad are continental rather than Caribbean. Trinidad and the adjacent island of Tobago are geologically part of South America rather than of the West Indies, and the faunistic and floristic character of the two islands is decidedly related to Guiana and Venezuela.

Our own collecting almost without exception has been confined to the Arima Valley in the Northern Range of Trinidad. However, Kaye & Lamont (1924) listed the species known to occur on the island as a whole and Lamont & Callan (1950) added two species to the Euchromiinae. The species reported by these authors are included in this paper. There are extremely few records from the southern part of the island and additional species may be expected when this region has been investigated.

My thanks go to Miss Rosemary Kenedy, who made notes and took photographs of many of the holotypes of the ctenuchid species in the British Museum (Natural History) which aided in the determination of some of the species in question. She also collected the majority of the department's ctenuchid collection. Thanks go also to Dr. William Beebe and Miss Jocelyn Crane for their part in assembling the collection and for advice and criticism.

EUCHROMIINAE

The absence of vein Sc in the hindwing separates the Euchromiinae from other families of Trinidad moths. In this subfamily vein M₂ of the hindwing is rudimentary or absent but often represented by a vein-like line of scales, whereas

in the subsequent subfamily, Ctenuchinae, vein M₂ of the hindwing is present. Veins Cu₁ and Cu₂ are stalked or united in the Euchromiinae, but in the Ctenuchinae, with the exception of the *Horama* and related genera, they are widely separated.

PSEUDOSPHEX Hubner

This and the following two genera are wasp-like in appearance, with constricted abdomens.

Pseudosphex kenedyae, new species

(Pl. I, fig. 1; Pl. II, fig. 1)

Pseudosphex melanogen Beebe, not Dyar, 1955: 32, fig. 6.

Length of forewing 11 mm.

Closely related to *Pseudosphex laticincta* Hampson. *P. kenedyae* differs from *P. laticincta* principally in lacking the dorsal band on the first abdominal segment and on the lateral bullae.

Male.—Antennae bipectinate. Processes on first segment of antennae small but gradually increasing in length to the seventh segment where it reaches a length of .142 mm. The processes are but slightly dilated, pubescent anteriorly and with a bristle at the distal end. Near the distal third of the antennae the pectinate processes decrease in length and resolve into three dentate segments followed by 14 serrate segments. The serrate segments are blackish-brown and the remainder of the antennae reddish-brown.

Palpi concolorous yellow with a fan-shaped tuft of hairs on the basal palpal segment yellow interspersed with black hairs. Front yellow but in rubbed specimens may have a whitish cast. A large black spot on vertex of head surrounded by yellow. Side of head behind eyes yellow with occasional black hairs or scales.

Patagia yellow with a broad black bar behind middle. Tegulae yellow edged with black; broadly edged with black at the costal margin of the forewing where it projects slightly on the subcostal and cubital veins. Mesothorax (scutum) black with two diagonal yellow stripes and a mid-dorsal line of yellow scales broadening caudally. Hind edge of scutum with yellow scales. Metathorax yellow.

Legs yellow. The inner face of the forecoxae shining white. The distal edge with a few scattered yellow scales. Inner face of forefemur shining white but somewhat variable in width in different lights, with the cephalad edge yellow. Frequently on the outer edge of the distal tip of the femur of the meso- and metathoracic legs a very small patch of shining white scales.

In different lights the yellow color of the thoracic structures may take on an orange-yellow cast.

Forewing hyaline. Costal area, area beyond discal cell, part of discal cell above discal fold and area below vein 2dA fuscus brown. Remainder of wing with scattered setae.

Hindwing hyaline with scattered setae except the costal area above the cell and vein R_s which is fuscus, similar in color to the respective area of the forewing.

Dorsum of first abdominal segment and bullae yellow with the anterior margin finely edged with black. Second abdominal segment (peduncle) translucent yellow. *The subsequent caudal segment with the anterior half tan brown and the posterior half translucent yellow.* The mid-dorsum of this segment may have a slight mid-dorsal line of darker scales. Fourth, fifth and sixth segments of the abdomen with the two-thirds of the cephalad portion of the segment blackish-brown and the caudal third translucent yellow. Seventh abdominal segment dark and yellow area approximately equal. Last segment with only the cephalad quarter of the segment blackish-brown. Terminal tuft of the abdomen yellow.

Ventrum of the abdomen with the anterior part of the valve (peduncle) relatively unscaled, usually gray but sometimes dark brown. Often with scattered occasional yellow scales. Approximately at the point where the caudal lateral edge of the dorsal sclerite of the peduncle segment touches the ventral vein, the valve becomes translucent yellow. The valve is fringed on its caudal edge with white scales approximately a fifth of the length of the yellow part of the valve. Remainder of the ventrum yellow peppered with black scales.

Female similar to the male except wing expanse greater (12 mm.), and the basal and medial part of the antennae prismatic. The last 12 distal antennal segments are slightly serrate, dark grayish-brown in our single female and the three preceding segments light brown and dentate rather than prismatic. The remaining segments of the antennae are warm reddish-brown. The legs are concolorous yellow with no white areas.

Closely related to *P. laticincta* from which it differs by having a concolorous first abdominal segment and bullae whereas in *P. laticincta* the first abdominal segment has a dorsal stripe and the bullae are banded.

Rosemary Kenedy compared part of our series with Hampson's type of *P. laticincta* in the British Museum (Natural History) and noted that in the male of *P. kenedyae* the antennal shaft is darker than the type of *P. laticincta* so that the basal darkening is not so apparent. *P. kenedyae* has a longer and more

restricted antennal extremity preceded by a contrasting lighter area and the pectinations slightly longer and not so dilated. The light brown abdominal band on the second segment of *P. kenedyae* is a black band in *P. laticincta* and the same color as the subsequent black abdominal bands. The dark abdominal bands of *P. laticincta* are narrower and extend to slight points behind mid-dorsally, more so than in *P. kenedyae*. In *P. kenedyae* only the fifth and sixth abdominal segments consistently have pronounced black points.

It is also important to note from Miss Kenedy's memoranda that the palpi of *P. laticincta* are similar to *P. kenedyae*. The palpi are yellow with a fan-shaped process from the basal palpal segment with yellow scales interspersed with black scales. In other words, the palpi are not banded in the usual meaning of the term in *P. laticincta*, as the original description would lead one to believe.

P. kenedyae differs from *P. melanogen* Dyar in having more yellow on the thorax and much wider yellow bands on the abdomen. The same considerations are true for *P. deceptans* Zerny which was synonymized under *P. melanogen* by Hampson. Neither *P. melanogen* nor *P. deceptans* are described as having white forecoxae.

For purposes of Trinidad identification, the broad fuscus costal margin of the forewing will separate this species from the species in the following two genera.

I take pleasure in naming this species for Miss Rosemary Kenedy, Research Assistant of the Department of Tropical Research, whose initiative in the use of *Heliotropium* as an attractant for euchromids brought to light this new species.

Material—All of the types were taken at Simla, Arima Valley, Trinidad, on *Heliotropium indicum*. Holotype, male, Catalog No. 5639, 20-II; allotype, female, (5640) 29-IV; 15 paratypes, males, (5641) 14-I, (5642) 15-I, (5643) 20-I, (5644) 28-I, (5645) 10-II, (5646) 20-II, (5647) 22-II, (5648) 23-II, (5649) (5650) (5651) 4-IV, (5652) 29-IV, (5653) 1-V, (5654) 27-XII, (5655) 31-XII.

Disposition of type material.—The Department of Tropical Research, New York Zoological Society, will retain three paratypes, Catalog Nos. 5650, 5651 and 5655. Paratypes with Catalog Nos. 5648 and 5653 are in the British Museum (Natural History) collection and paratypes with Catalog Nos. 5644 and 5652 are in the United States National Museum collections. The holotype, allotype and remaining paratypes are in the American Museum of Natural History, New York.

PLEUROSOMA Orfila

This and the following genus may be distinguished from the preceding genus, *Pseudosphex*, by vein R₅ of the forewing arising basad of vein R₃.

The genus *Astridia* Kiriakoff, 1948: 267, is an absolute synonym of *Pleurosoma* Orfila, 1935: 178.

Both genera were erected with *Sphecosoma angustatum* Moschler as the type.

Pleurosoma trinitatis (Rothschild)
(Pl. III, fig. 1)

Sphecosoma trinitatis Rothschild, 1911: 24.

Sphecosoma trinitatis, Rothschild, 1913: 471, pl. XIV, fig. 5.

Sphecosoma trinitatis, Hampson, 1914: 90.

Sphecosoma trinitatis, Draudt, 1915: 40, fig. 10h.

Sphecosoma trinitatis, Kaye & Lamont, 1927: 1.

Pleurosoma trinitatis, Orfila, 1935: 178.

Described by Rothschild from four male specimens collected at Caparo, Trinidad, in December, 1905, by S. M. Klages.

The figures in Rothschild and Seitz are misleading, for they indicate that the color of the abdominal segment following the peduncle is black, similar to the subsequent segments, rather than rufous brown. The length of the forewing in our specimens is 12 mm. The length of the forewing of the holotype in the British Museum is 12 mm., rather than the 14 mm. given by Rothschild.

Female similar to male except antennae prismatic rather than bipectinate.

Material.—Fifteen males and eight females.

Range.—Trinidad.

SPHECOPS Orfila

Differs from *Pleurosoma* in lacking the two thoracic bladder-like processes beneath the base of the first abdominal segment. First segment of abdomen much shorter in *Sphecops* than *Pleurosoma*. The males of *Sphecops* have a ventral valve covering the second and third abdominal segments which is absent in *Pleurosoma*.

Sphecops aurantiipes (Rothschild)
(Pl. III, fig. 2)

Sphecosoma aurantiipes Rothschild, 1911: 25.

Sphecosoma aurantiipes, Rothschild, 1913: 471, pl. XIV, fig. 7.

Sphecosoma aurantiipes, Hampson, 1914: 91.

Sphecosoma aurantiipes, Draudt, 1915: 40, fig. 10h.

Sphecosoma aurantiipes, Orfila, 1935: 181.

Four of our Trinidad specimens have been compared with Rothschild's type from San Esteban, Venezuela, in the British Museum by Miss Rosemary Kenedy. Rothschild gives the length of the forewing as 14 mm. in his original description, whereas our measurement of the type is 12.5 mm. The Trinidad specimens have a forewing length of 10 to 11 mm. In this respect they resemble material that Rothschild had before him from Paraguay and Bolivia which he reported as having a wing length of 10 mm. The yellow bands on the abdomen of the Trinidad specimens are narrower than in the type from Venezuela.

Material.—Seven males.

Range.—Venezuela, Paraguay and Bolivia. A new record for Trinidad.

HOMEOCERA Felder

A genus related to *Gymnelia*, consisting of large, heavy-bodied species. We have not taken any species of this genus in the Arima valley.

Homoeocera magnolimbata Dognin

Homoeocera magnolimbata Dognin, 1911: II:3.

Homoeocera magnolimbata, Hampson, 1914: I:95, pl. V, fig. 1.

Homoeocera magnolimbata, Draudt in Seitz, 1915: VI:46, pl. 27b.

Kaye & Lamont (1927) report this species from Trinidad. One specimen appears to have been taken in Trinidad by F. W. Urich at St. Ann's in October, 1899. This specimen is not in the Urich Insect Collection at the Victoria Museum in Port-of-Spain. It is a large insect, approximately two inches in expanse, with hyaline wings and black abdomen with conspicuous white spots and some metallic blue.

Kenedy reports another specimen from Trinidad in the British Museum (Natural History) in the Joicey Collection, collected in 1909. It was part of a series from French Guiana, Amazons, East Bolivia and Peru.

ISANTHRENE Hubner

The thorax of the species in this genus is smoothly scaled in contrast to the species of *Homoeocera* which have hairy thoraxes.

Isanthrene tryhanei Rothschild

Isanthrene tryhanei Rothschild, 1911: XVIII: 26.

Isanthrene tryhanei, Rothschild, 1913: XX: 471, pl. XIV, fig. 24.

Isanthrene tryhanei, Hampson, 1914: I: 98.

Isanthrene tryhanei, Draudt in Seitz, 1915: VI: 47, pl. 10b.

Rothschild described this species from St. Ann's, Trinidad, from one female. It does not appear to have been collected since the original specimen was taken. It is another large species approximately two inches in expanse, with hyaline wings. The wings have a yellowish cast particularly along the costal and inner margin, in contrast to *Homoeocera magnolimbata*.

PHOENICOPROCTA Druce (not Hampson)

Stephens (1850) used the name *Hyela* for a generic name in Noctuidae. Walker (1854) used *Hyela* for one of his groups in the genus *Glaucopis* with the intention that the species he placed under *Glaucopis* would henceforth take the various group names as generic names. Hampson (1898) realized that Walker had employed a name, *Hyela*, that was preoccupied by Stephens, and erected a new name *Phoenicoprocta*. Druce (1898) was apparently cognizant of Hampson's monograph of the Ctenuchidae and described a presumed new species, *Phoenicoprocta metachrysea*. This species employing Hampson's new name was published in May, 1898, in advance of Hampson's monograph, which was not published until September, 1898. Thus Druce must be credited with the generic name *Phoenicoprocta*. The type of the genus is *Phoenicoprocta metachrysea* by monotypy which Dyar (1915) synonymized under *Phoenicoprocta vacillans* Walker (1856) on the basis of breeding carried out by H. W. B. Moore in British Guiana.

The males of this genus are easily distinguished in Trinidad by the blue or red spotted abdomen and carmine anal tufts. The *Aethria* species with a carmine tuft have a concolorous blackish abdominal dorsum. The females have a *Calonotus*-like abdomen and may be distinguished from *Calonotus* by vein R_2 in *Phoenicoprocta* being forked with veins R_{3+4+5} rather than from the cell as in *Calonotus*.

Phoenicoprocta vacillans (Walker)

Pl. III, figs. 3, 4, 5

Eunomia vacillans Walker, 1856: VII: 1617 (male).

Phoenicoprocta vacillans, Hampson, 1898: I: 197, pl. VII, fig. 11 (male).

Phoenicoprocta vacillans, Draudt in Seitz, 1915: VI: 47, pl. 12a (male). 1917: Supp.: 199.

Phoenicoprocta metachrysea Druce, 1898: (7) I: 404 (male).

Phoenicoprocta metachrysea, Hampson, 1898: I: 196, pl. VII, fig. 12 (male).

Phoenicoprocta metachrysea, Draudt in Seitz, 1915: VI: 47, pl. 12a; (male). 1917: Supp.: 199.

Phoenicoprocta chrysorrhoea Hampson, 1898: I: 196 (male).

Phoenicoprocta chrysorrhoea, Draudt in Seitz, 1915: VI: 57, pl. 12a (male). 1917: Supp.: 199.

Phoenicoprocta trinitatis Strand, 1915: 21 (male).

Phoenicoprocta trinitatis, Draudt in Seitz, 1915: VI: 58, pl. 27f (male).

Phoenicoprocta nigropeltata Strand, 1915: 22 (male).

Leucotmemis albigutta Schaus, 1905: XXIX, No. 1420: 185 (female).

Leucotmemis albigutta, Hampson, 1914: Supp. I: 151, pl. VIII, fig. 2 (female).

Leucotmemis albigutta, Draudt in Seitz, 1915: VI: 70, pl. 27k; 1917: Supp.: 201 (female).

Leucotmemis thoracica Schaus, 1905: XXIX, No. 1420: 186 (female).

Leucotmemis thoracica, Hampson, 1914: Supp. I: 150, pl. VIII, fig. 1 (female).

Leucotmemis thoracica, Draudt in Seitz, 1915: VI: 70, pl. 27k; 1917: Supp.: 201 (female).

Antichloris trinitatis Rothschild, New Syntomidae. 1912: XIX: 154 (female).

Autochloris trinitatis, Hampson, 1914: Supp. I: 104, pl. V, fig. 17 (female).

Antichloris trinitatis, Draudt in Seitz, 1915: VI: 136 (female).

Autochloris trinitatis, Draudt in Seitz, 1917: VI: Supp.: 197, pl. 27c (female).

Paramya chrysonota Hampson, 1898, I: 165, pl. VII, fig. 3 (female).

Paramya chrysonota, Draudt in Seitz, 1915: VI: 44, pl. 10k (female).

Calonotus hoffmannsi Rothschild, 1911: XVIII: 30 (female).

Calonotus hoffmannsi, Rothschild, Some unfigured Syntomidae, 1913: XX: 470, pl. XIII, fig. 35 (female).

Leucotmemis hoffmannsi, Hampson, 1914: Supp. I: 150 (female).

Paramya? hoffmannsi, Draudt in Seitz, 1915: VI: 44 (female).

Calonotus hoffmannsi, Draudt in Seitz, 1915: VI: 108, pl. 17k; 1917: Supp.: 201 (female).

Antichloris trinitatis, Kaye & Lamont, 1927: No. 3: 9.

Phoenicoprocta trinitatis, Kaye & Lamont, ibid: 1927: 1.

Phoenicoprocta rubiventer? Kaye & Lamont, 1927: 1.

Mydropastea chrysonota, Kaye & Lamont, 1927: 1.

The extreme variability of this species is indicated by the above synonymy, which undoubtedly is incomplete. Species designation has been based on the color of the collar, shoulder-covers, thorax, legs, abdomen and the ventral valve at the base of the abdomen in the males; and in the females, aside from the fact that they have been placed in the wrong genera, largely on the amount of hyaline areas in the wings.

In all of our specimens of *Phoenicoprocta* from Trinidad, British Guiana and Venezuela, and specimens loaned to us by the American Museum of Natural History from Mexico, British Guiana, Brazil and Peru, there is a small accessory cell in the forewing formed by a sectorial cross-vein between vein R_2 and vein R_{3+4+5} . This sectorial cross-vein emerges from R_{3+4+5} typically at the same point at which vein R_5 forks but may vary to the extent of being one millimeter more basad. Hampson (1898, p. 196) makes no mention of this cross-vein, which appears to be a good generic character. In addition, he states that vein 3 (vein Cu_1) of the hindwing is absent whereas it is invariably present though shortly stalked near the margin of the wing.

Furthermore, the genus is not divisible into two sections on Hampson's characters. In the species that he places in the first section, the discocellulars in the hindwing are not oblique throughout while in the forewing, vein 3 (vein Cu_1) is variable in a series from the same locality.

The commonest form at Simla, Trinidad, is *nigropeltata* Strand which was described from Trinidad. The character distinguishing this form from the typical *vacillans* is a black ventral valve with a white posterior edge, rather than a white valve with a black base and lateral edges. We have fifteen specimens that agree with this diagnosis of *nigropeltata*, but in four additional specimens the white edge is replaced by pink. Hampson (1898, p. 197), in his diagnosis of *vacillans*, stated "forecoxae white and crimson" (forecoxae white, red inside, as Kenedy noted on holotype). Eight of our 19 specimens agree in this respect, although more pink than red, and the remaining 11 specimens have the coxae white in front and blackish-brown inside. Four of these latter specimens have the pink-edged valve.

Ten additional specimens appear to be *trinitatis* Strand. This species is described as having short palpi. In our specimens the palpi appear to be the usual length. The origin of vein Cu_1 in the forewing is variable. The amount, position and presence of blue, crimson and black on the collar are extremely variable, encompass-

ing *trinitatis*, *sanguinea* and new forms. The colors of the patagia and tegulae vary considerably in different lights because of their iridescent cast alone. The subdorsal macular stripes on the abdomen also vary considerably; sometimes they are large and distinct and in others, particularly near the base of the abdomen, they may be quite small. The ventrum of the abdomen in these specimens varies between black and blackish-brown. The ventral valve is light to dark pink and in one specimen with a considerable mixture of black scales. The posterior edge of the valve is finely white. The forecoxae in these ten specimens are white. The inside of the forecoxae and the remaining coxae usually red but sometimes blackish-brown.

In an additional specimen, an eleventh specimen, the shoulder covers are dark brown, forecoxae white and remaining coxae blackish-brown, the last four abdominal segments with a macular red subdorsal line and the ventral valve black with a white edge. This specimen is an unnamed, more melanotic, form of the preceding ten specimens.

Two specimens are very similar to *sanguinea* Walker. Our specimens differ in having a black transverse line at the base of the anal tuft and a narrower discocellular bar in the forewing. In the forewings of *sanguinea* Walker there is a small hyaline spot above vein R_5 which is definitely absent in all of our specimens. In Draudt's figure in Seitz (fig. 15a; 1915) the shoulder covers and the abdomen are reddish-brown rather than the correct color, crimson. Hampson (p. 198, 1898) gives the type locality as Honduras. Walker (1854, p. 172) in his original description did not state the origin of his specimen. The holotype in the British Museum (Natural History) has a hand-printed label "Honduras" in neither Walker's nor Hampson's writing.

The sexes in *Phoenicoprocta vacillans* are dimorphic. Besides, the amount of scaling in the wings of the females in Trinidad is extremely variable.

The female specimens will run in Hampson's generic key (1898) to *Mydropastea* (*Phaeo*) or *Paramya* (*Methysia*) since Hampson's dichotomous couplet (1898: 23 (B, a^4), 24 (b^4)) is based on the presence of abdominal tufts which are a male character. The abdominal aspect of the females differs radically from that of the males, which have a typically maculated series of red or iridescent blue spots whereas the females have blackish and iridescent blue longitudinal stripes. The abdomens of both males and females are somewhat bulbous caudad of the third or fourth abdominal segments.

The abdomens of all the female specimens are similar in showing a mid-dorsal stripe of iridescent blue or blue-green scales. This line is continued on the metathorax, which has a single mid-dorsal spot of the same color. The mid-dorsal stripe of the abdomen is bordered by a blackish-brown stripe on each side commencing on the first abdominal segment and followed laterally by another stripe of iridescent blue or blue-green which is replaced on the first abdominal segments by iridescent spots on a blackish-brown ground. Laterally the last subdorsal iridescent stripe is bordered by a fine blackish-brown line. In old or rubbed specimens the iridescence of the abdomen may have a coppery cast. The ventrum of the abdomen is dark brown to brownish-black and iridescent in some lights. There are iridescent blue points beneath the wings on the thorax and a line of iridescent blue on the caudal edge of the metathorax continuous from each side. The amount of carmine on the under side of the coxae is variable but is present in all female specimens on the distal end of the prothoracic coxae and frequently on the whole underside of the forecoxae but usually only at the distal apex of the meso- and metathoracic coxae. The anterior surface of the prothoracic coxae is marked with iridescent blue on a brown background, most distinct on the outer edge of the coxae.

Female Form I.—Two specimens. Both the fore and hindwings of this form are immaculate blackish-brown with no hyaline spots whatsoever. Some blue scales along the radius vein of the forewing. Kenedy compared this form with the holotype of *Antichloris trinitatis* Rothschild in the British Museum (Natural History) and believes them to be identical.

Female Form II.—This form differs from Form I in having a short elliptical hyaline spot below the middle of the cell and hyaline spots below the cell on each side of vein M_3 in the forewing. The hindwing has a hyaline spot below the cell, a small spot at the forking of vein Cu_{1+2} and vein M_3 and a large spot above vein M_3 to vein M_1 . This last mentioned hyaline spot decreases in size approximately one-third above the line of scales representing vein M_2 . One of the three specimens has crimson patagia. The abdominal and wing patterns of this form are similar to the figure in Draudt in Seitz (pl. 101; 1915) of *Mydropastea chrysonota* Hampson.

Female Form III.—Differs from Form II in having two or three small hyaline spots above the larger hyaline spots on each side of vein M_3 of the forewing. The spot anterior to the large spot in cell M_2 , if present, is minute. The hyaline area beneath the discal cell is larger and may extend slightly below the anal vein. A slight

hyaline streak within the discal cell along the cubital vein. In the hindwing the hyaline spot below the cell is larger than in Form II and may extend slightly below the anal vein.

Female Form IV.—Three specimens were taken of this form. The hyaline areas in the forewing are progressively more extensive by the addition of a hyaline spot in the forewing between veins Cu_1 and Cu_2 , a large hyaline streak below the anal vein and the posterior portion of the discal cell. In the hindwing the hyaline area extends below the anal vein. None of the above four female forms is to be interpreted as being stable, as they grade into one another.

Paramya chrysonota Hampson is a synonym of *Phoenicoprocta vacillans* Walker. One specimen of *chrysonota* was collected at Itaituba, Amazons, Brazil, and described as a male. Kenedy inspected the holotype of *chrysonota* in the British Museum (Natural History) and discovered that, in point of fact, it is a female rather than a male. It agrees with our female series in Form II from Simla, Trinidad.

Some discussion of the past history of *Paramya chrysonota* would not be out of place. Section I of *Paramya* Hampson (p. 164; 1898) establishes with *Paramya intersecta* Hampson (p. 164; 1898) as the genus type is synonymized by Hampson (p. 384; 1914) under *Methysia* Butler with the genus type species *Methysia (Glaucopis) notabilis* Walker (1854) on the basis that Hampson's figure (fig. 205, 1898) of *Methysia notabilis* is correct. Thus *Methysia* contained the following species: *notabilis* Walker, *intersecta* Hampson, *senetus* Schaus, *picta* Druce and *melanota* Hampson. This left *brice-noi* Rothschild, *flavia* Schaus, *picta* Druce and *chrysonota* Hampson with no proper generic name as these species were in Hampson's section II of the genus *Paramya*.

However, Hampson was not the legitimate author of *Paramya* nor was he privileged to select a type species, as Druce in May of the same year (1898) and also, for that matter, Schaus in June had each described new species employing the generic name *Paramya*. Hampson in his *Cat. Lep. Phal.* I, published in September, included both Druce's and Schaus's new species in the second section of his presumed new genus. Neither Druce nor Schaus wrote generic descriptions and what apparently happened was that both were familiar with the new genus that Hampson was to erect in his monograph and described their new species in that genus. Unfortunately their descriptions were published a few months previous to Hampson's monograph. The type species of *Paramya* is *Paramya picta* Druce.

However, *Paramya* was preoccupied by Conrad (1860) in Mollusca and, consequently was unavailable for Druce's species. Travassos (1946) erected a new name, *Metamya*, for *Paramya* Druce. The genotype is *Metamya picta* Druce, and *Paramya flavia* Schaus and *Ichoria bricenoi* Rothschild are congeneric. *Paramya chrysonota* Hampson (1898), with which we are concerned, is not congeneric with either section of Hampson's original conception of the genus and is a female *Phoenicoprocta*.

Kaye & Lamont (1927) placed *Paramya chrysonota* Hampson (1898) in the genus *Mydropastea* Hampson (1898). I presume they did this because *Paramya* as conceived by Hampson has veins R_s and M_1 of the hindwing long stalked. Apparently the specimens that Kaye & Lamont possessed from Trinidad resembled our specimens from Trinidad in which veins R_s and M_1 are approximate. Thus, they placed the species in *Mydropastea*, albeit incorrectly.

In Hampson's Supplement (p. 209; 1914) he synonymized his genus *Mydropastea* (1898) under *Phaio* Neumoegen (1894). Draudt in Seitz picked up the synonymy but changed the spelling of the genus to *Phaëo* following Wagner (1912).

Calonotus hoffmannsi Rothschild (1911) is a synonym of *Phoenicoprocta vacillans* Walker. Draudt in Seitz (p. 108, 1915; p. 201, 1917) was correct in his suggested synonymy, namely, *Calonotus hoffmannsi* (1911) is a synonym of *Paramya chrysonota* (1898). Hampson in his Supplement (p. 150; 1914) placed *hoffmannsi* in *Leucotmemis*. *Calonotus hoffmannsi* was described from Itaituba, Brazil, the same type locality as *Paramya chrysonota*.

The male genitalia of the specimens from Trinidad, two from Caripito, Venezuela, and a specimen from British Guiana are similar. However, the genitalia of two specimens, one from Candelopa, Peru, and another from Pitaguaya, Bolivia, while very similar in other respects, have a distinctly different pair of protuberances on either side of the base of the uncus. They are rounded and bulbous in the latter specimens and pointed in our *vacillans*. The general facies of the Peruvian and Bolivian specimens appears to be the same as our material.

Judging from the preceding discussion it is quite likely that a large number of the species described in *Phoenicoprocta* will be synonymized. It is necessary, however, to study genitalia of the holotypes or in lieu of that, of topotypical material. In the subsequent paragraphs I shall give an indication of the probable disposition of some of the species of *Phoenicoprocta*.

Phoenicoprocta mexicana (Walker) will have to be removed from the genus. The sexes are not dimorphic. The wing venation differs in the forewing by lacking the sectorial vein in the radials. It differs in the hindwing by veins Cu_1 and Cu_2 being completely united and veins R_s and M_1 being approximate, not connate or very shortly stalked.

Forbes (1930) correctly removed *Zygaena parthenii* Fabricius from the genus *Mallodeta* where Hampson (1898) placed it. Nonetheless, it does not appear to be a *Phoenicoprocta*. The venation differs in the forewing by lacking the sectorial vein of the radials. It also differs in the forewing in that vein R_5 forks from the radial midway between vein R_2 and the forking of veins R_3 and R_4 , whereas in *vacillans* it separates very near the forking of veins R_3 and R_4 . I have not seen a female nor has the female been described, so I do not know if the sexes are dimorphic. The hindwing of *parthenii* is similar in that veins Cu_2 and Cu_3 are forked near the margin of the wing and veins M_1 and R_s are slightly stalked.

Phoenicoprocta paucipuncta Dyar is not a *Phoenicoprocta* but probably, as Forbes (1939) suggests, a color form of *Cosmosoma gemmata* Butler.

The following species may well be only color forms of *vacillans*. Males: *rubiventer* Hampson from Panama; *sanguinea* (Walker), the species type for which Hampson gives the type locality as Honduras though Walker did not know the type locality in his original description, the hand-printed label on the holotype stating Honduras being in neither Walker's nor Hampson's writing; *astrifera* (Butler) from Braga (Amazons) Brazil; *haemorrhoidalis* (Fabricius) from Brazil; *flavipicta* Hampson from British Guiana; *variabilis* Kaye from from Panama; *intermedia* Forster from Venezuela and *nigriventer* Gaede from Venezuela; females: *biformata* Gibbs and the aberration *atrappennis* Strand from British Honduras; *insperata* (Walker) from Para, Brazil. *Phoenicoprocta astrifera* (Butler), as Draudt in Seitz figures it (pl. 12c; 1915), has wide terminal wing margins. The holotype has wing margins as in *vacillans*. The following were described as forms of *vacillans* and should be reappraised: *aurantipatagiata* Draudt, *auriflua* Draudt, *nigricoxa* Zerny and *punicea* Strand.

While I have seen no specimens from the West Indies, the form existing there appears to be a distinct species. Hampson (1914: 125) synonymized *thomae* (Lucas), *cubana* Druce and *selecta* (Herrich-Schaffer) under *capistrata*. Fabricius's type locality for *capistrata* is "America", which meant the mainland, and

Herrich-Schaffer's type locality for *selecta* is Brazil. Both are females and are more likely the female forms of *vacillans* while *exima* (Herrich-Schaffer), described from Cuba, is the actual female form from the West Indies. If the above suggestions prove to be correct, *thomae* (Lucas) has priority and *capistrata* (Fabricius) would preoccupy *vacillans* (Walker).

Phoenicoprocta jamaicensis Schaus is based on a female type. *Phoenicoprocta lydia* (Druce), with the synonyms *thera* (Druce) and *demonia* (Druce), is a distinct species from Mexico. It has the same fore- and hindwing venation as the *vacillans* we have from Trinidad and is sexually dimorphic in the same fashion.

The forms of *Phoenicoprocta* from South Brazil, Paraguay, Uruguay, Peru and Bolivia appear to be distinct from the forms found from the Amazons north. Jorgensen's species *schreiteri* and *sieboldi* appear to be the slight variants of *latimarginata* Gaede (1926). The wider margins of the wings alone would seem to distinguish these southern forms from *vacillans*. Two genitalia from Bolivian and Peruvian specimens that were mentioned before are distinct from *vacillans* though the facies of the insects are similar.

Phoenicoprocta teda (Walker) is a distinct species but quite possibly not a *Phoenicoprocta*.

LOXOPHLEBIA Butler

In our species of *Loxophlebia* the discocellulars are not oblique throughout in the hindwing as Hampson (1898: 206) states in his generic diagnosis. Furthermore, vein Cu₂ of the hindwing is present but very shortly stalked with vein Cu₁; the forking occurs at the inner edge of the black wing border. The following genera, *Mesothen* and *Loxophlebia*, may be separated from other Trinidad genera by vein M₂ of the forewing originating well above vein M₃, more than a third but less than half the distance up between veins M₁ and M₃. The same vein, M₂, in *Pheia* is approximately a fifth in our species. The genus *Mesothen* is very close to *Loxophlebia* and I am unable to separate these genera except superficially on the basis of the specimens on hand, so the following key will serve to distinguish the Trinidad species in both genera. Surinam and British Guiana forms of *Loxophlebia bisigna* in the key would run to *Mesothen aurantegula*, so I have included an additional couplet in the event that these forms are found in Trinidad in the future.

1. Abdomen with some red or orange color
2 (*Loxophlebia*)
Abdomen with no red or orange color
4 (*Mesothen*)

2. Abdomen with broad lateral orange bands
diaphana
Abdomen with no lateral bands of any color3
3. Abdomen blackish-brown with subdorsal white spots on basal segment and subdorsal red spots on fourth abdominal segment*bisigna* (Trinidad form?)
Abdomen black with the last four segments orange*postflavia*
4. Disc of thorax orange-red*pyrrha*
Disc of thorax black or blackish-brown..5
5. Tegulae with orange patches6
Tegulae concolorous brownish-black...7
6. Abdomen concolorous blackish-brown
aurantegula
Abdomen with subdorsal white spots on basal abdominal segments
bisigna (extra-limital forms)
7. Male with abdominal ventral valve. Female with white subventral abdominal band
endoleuca
Male without abdominal ventral valve.
Female without white subventral abdominal band*desperata*

Loxophlebia diaphana (Sepp)

Glaucoptis diaphana Sepp, 1848: II: 185, pl. 81.
Glaucoptis discifera, Walker, 1854: I: 178.
Laemocharis bura Butler, not Herrich-Schaffer, 1877: I: 33, pl. 11, fig. 12.
Chrysostola albifrons Moschler, 1872: XXXIII: 344.
Loxophlebia diaphana, Hampson, 1898: I: 209.
Loxophlebia diaphana, Draudt in Seitz, 1915: VI: 62, pl. 12g.
Loxophlebia diaphana, Kaye & Lamont, 1927: No. 3: 2.

We have not collected this species at Simla, but Norman Lamont collected a specimen at Palmiste in January, 1921.

Range.—Surinam and Amazons.

Loxophlebia bisigna (Kaye)
(Pl. III, fig. 6)

Pheia bisigna Kaye, 1911: XLIV: 146.
Pheia bisigna, Hampson, 1914: Supp. I: 128, pl. VI, fig. 17.
Loxophlebia klagesi Rothschild, 1811: XVIII: 29.
Loxophlebia klagesi, Rothschild, 1913: XX: 471, pl. 14, fig. 21.
Loxophlebia clagesi, Hampson, 1914: Supp.: 135.

Pheia bisigna, Draudt in Seitz, 1915: VI: 61; 1917: Supp.: 199, pl. 27f.

Loxophlebia klagesi, Draudt in Seitz, 1915: VI: 63, pl. 12g.

Loxophlebia bisigna, Kaye & Lamont, 1927: No. 3: 2.

I have followed Draudt's (1915, 1917) synonymy of this species. The abdominal characteristics of the original type material of *klagesi* are variable. Rothschild's paratype of *klagesi* from Caporo (*sic*. Caparo), Trinidad, is similar to our three specimens in having paired reddish subdorsal spots on the fourth abdominal segment. Two paratypes from Maripa, Caura River, Venezuela, have paired reddish spots on the third and fourth abdominal segments. The four Surinam types along with Kaye's holotype of *bisigna* from the Potaro River, British Guiana, lack these reddish spots. Kaye's *bisigna* was described two months earlier than Rothschild's *klagesi*. The label on the holotype of *klagesi* in the British Museum (Natural History) has on the locality label "Aroewarwa Creek, Maroewyn valley, Surinam, May 1905. (S. M. Klages)" whereas in Rothschild's original description the material from this locality is given as February.

Range.—Trinidad, Venezuela and Guianas.

Loxophlebia postflavia Druce
(Pl. III, fig. 7)

Loxophlebia postflavia Druce, 1898: I: 407.

Loxophlebia postflavia, Hampson, 1898: I: 210, pl. VIII, fig. 4.

Loxophlebia postflavia, Druce in Seitz, 1915: VI: 64, pl. 12h.

Two specimens were collected. This is a new record for Trinidad.

Range.—Described from French Guiana. Specimens in British Museum from British Guiana and Surinam.

MESOTHEN Hampson

In this genus, as in the former genus, Cu_1 and Cu_2 of the hindwing are forked within the dark terminal band. Thus Cu_2 is present, not absent, as stated in Hampson's original description (p. 212; 1898). The species of this genus have been keyed in the genus *Loxophlebia*.

Mesothen aurantegula (Jones)

Loxophlebia aurantegula D. Jones, 1914: 4, pl. 1, fig. 6.

Mesothen aurantegula, Hampson, 1914: Suppl. I: 146, pl. VII, fig. 25.

Mesothen aurantegula, Draudt in Seitz, 1917: VI: 200, pl. 27h.

Mesothen aurantegula, Kay & Lamont, 1927: No. 3: 2.

An unusual record based on one specimen collected by Norman Lamont at Palmiste in January. The species was described from one female taken at Santos, southern Brazil.

Range.—Southern Brazil and Trinidad.

Mesothen endoleuca Druce
(Pl. III, fig. 8)

Mesothen endoleuca Druce, 1905: XV: 460.

Mesothen endoleuca, Hampson, 1914: Suppl. I: 146, pl. VII, fig. 27.

Mesothen endoleuca, Draudt in Seitz, 1915: VI: 66, pl. 27i.

Female with a ventrolateral band of white scales on abdomen, broadest at the base of the abdomen. Black border at the apex and margins of the forewing much wider than in male. Forecoxae white in both sexes.

Eleven specimens were collected, of which five were females.

Range.—Venezuela. A new record for Trinidad.

Mesothen desperata (Walker)

Pseudomya desperata Walker, 1856: VII: 1602.

Mesothen desperata, Hampson, 1898: 215, pl. VIII, fig. 3.

Mesothen desperata, Hampson, 1914: 146, fig. 20.

Mesothen desperata, Draudt in Seitz, 1915: 66, pl. 27l.

Mesothen desperata, Lamont & Callan, 1950: 197.

One specimen reported by Lamont & Callan (1950: 197) was collected by Lamont in April at Palmiste. It is an aberrant species for the genus as the male lacks a ventral valve according to Hampson (1914: 146). Since our females of *endoleuca* have a ventrolateral band broadest at the base of the abdomen, not mentioned in the description of *desperata*, I have used this character in the key to separate the female specimens of these two species.

Range.—Panama, Guianas, Brazil, Paraguay and Argentina.

Mesothen pyrrha (Schaus)
(Pl. III, fig. 9)

Dycladia pyrrha Schaus, 1889: V: 89.

Dycladia pyrrha, Druce, 1896: II: 348, pl. 71, fig. 27.

Mesothen pyrrha, Hampson, 1898: I: 214.

Mesothen pyrrha, Draudt in Seitz, 1915: VI: 66, pl. 12i.

Mesothen pyrrha, Kaye & Lamont, 1927: No. 3: 2.

Only one of our male specimens has the valve white. In the remaining specimens it is brown with the margins at the base of the valve broadly and irregularly white. Only the proximal end of the coxae is white, while the remainder of the coxae is brown.

Material.—Four males and one female.

Range.—Mexico to Peru and the Guianas.

PHEIA Walker

Very close to *Cosmosoma* but the lower side of the discal cell is very short and the discocellular veins oblique. The only Trinidad species is considerably smaller than any of the Trinidad *Cosmosoma*. The wingspread of the smallest Trinidad species of *Cosmosoma*, *klagesi* and *remotum*, is 32 mm. whereas the following species is 22 mm.

Pheia beebei, new species
(Pl. I, fig. 2; Pl. II, fig. 2)

Length of forewing of male 11-12 mm., of female 13 mm.

Closely related to *Pheia gaudens* (Walker), from which *beebei* differs in its smaller size and narrower apical black patch on the forewings. *Pheia gaudens* was described from Para, Brazil, and has been reported from Venezuela and Peru.

Antennae bipectinate with a tuft on the apex of each pectination. Pectinations along shaft of antennae on the respective sides of the antennae of similar length except near base and apex. Pectinations on outside of antennal shaft slightly longer than on the inside. Shaft of antennae of male blackish-brown and of female brown. Scape of antennae with bright yellow tuft of scales most conspicuous on the inside anterior edge.

Palpi, front of head and behind eyes bright yellow. Basal segment of palpi clothed with long hair of irregular length, thus somewhat ragged in appearance. The remaining two segments of palpi finely scaled and upturned to vertex of head. Vertex of head black with some scattered iridescent blue scales most conspicuous in the center.

Collar bright yellow. Tegulae bright yellow, finely edged with black scales on the outside and broadly edged with black on the inside edge. A patch of iridescent blue scales within the black border of the inside edge.

Dorsum of the mesothorax yellow and of metathorax iridescent blue. Caudal edge of meta-

thorax with a narrow line of bright yellow scales. Pleura and ventrum of thorax bright yellow. Legs yellow with small brown patches on the mesothoracic and metathoracic legs. Forecoxae immaculate bright yellow. Some brown on distal segments of all tarsi.

Veins and margins of wings brown-black. Margins of wings narrow but broadening at apex of forewings (.91 mm. along vein R_5). In the forewing the Sc vein and area between discal cell and Sc vein to slightly beyond the end of the cell yellow. A small patch of yellow at base of wing between the discal cell and a line of black scales marking the anal wing fold. Another yellow patch more densely scaled between the wing fold to slightly beyond vein 2dA and terminating distally at a small black patch which lies on the anal fold. The distal end of the small black patch is slightly more than 2 mm. from the base of the wing. Some scattered black scales on the part of vein 2dA which extends into the yellow basal patch, but the basal part of the vein yellow. Scales representing vein M_2 extend within the discal cell for approximately half the length of the cell.

Hindwing with creamy yellow patch at base of wing extending along anterior part of discal cell for two-thirds the length of cell. The black margin of the wing diminishing gradually and disappearing completely near the base of the wing. This part of the wing is normally hidden beneath the forewing. The creamy patch extends within the base of the cell and terminates at a small black spot. Area below discal cell hyaline. A small streak of yellow scales in brown-black anal margin at base of wing.

Basal segment of abdomen including bullae bright yellow but each of the subsequent segments except the terminal segment with the anterior margin bright yellow and posterior margin brown-black. These latter brown-black bands expanding into triangular marks on the dorsum and obliterating the yellow on the mid-dorsum. The brown-black bands have scattered patches of iridescent blue or blue-green scales in various lights. The terminal segment of the abdomen is brown-black. Ventrum of abdomen yellow.

I take pleasure in naming this species after William Beebe, Director Emeritus of the Department of Tropical Research, New York Zoological Society.

Material.—All types were taken at Simla, Arima Valley, Trinidad. Holotype, male, Catalog No. 57207, 16 XII; 2 paratypes (57208) 15-I and (57209) 21-I.

Disposition of type material.—The Department of Tropical Research, New York Zoological Society, will retain two paratypes, Catalog

Nos. 57208 and 57209. The holotype, Catalog No. 57207, is in the American Museum of Natural History.

CHROSTOSOMA Hubner

Distinctive in this group of genera by having vein R_1 of the forewing stalked with the other radial veins and not free from the cell.

Chrostosoma viridipunctatum Rothschild (Pl. III, fig. 10)

Chrostosoma viridipunctatum, Rothschild, 1911: 30.

Chrostosoma viridipunctatum, Rothschild, 1913: 471, pl. XIV, fig. 34.

Chrostosoma viridipunctata, Hampson, 1914: 148.

Chrostosoma viridipunctatum, Draudt in Seitz, 1915: 67, pl. 12k.

Without an examination of the genitalia of the holotype in the British Museum (Natural History), it is impossible to be certain of the above identification. A genitalic examination of all the echemus-like species of this genus is necessary to determine the valid species and their respective ranges.

Hampson's (1898: 215) division of the genus into two sections on the basis of the presence or absence of vein Cu_1 in the hindwing is incorrect, as this vein is only forked nearer the margin of the wing in the first section than in the second section of the genus. Kenedy found that the holotypes of *decisum* and *viridipunctum* had both preserved vein Cu_1 .

The series of *viridipunctatum* in the British Museum (Natural History) contains three female specimens from Trinidad, one from Caparo and two from Tabaquite. One of the latter specimens has metallic coloring similar to Rothschild's type, whereas in our series of males and females any metallic coloring if present is slight. In this same British Museum series are specimens from Argentina, Paraguay, southern Brazil, French Guiana and Surinam containing both males and females.

The holotype is a female. The type locality is Yungas de la Paz, Bolivia, 1,000 meters.

In our series of *viridipunctatum* the iridescent blue, while variable, is never pronounced. Some iridescent blue on the front and vertex of the head, collar and shoulder covers and faint traces on the subdorsum of the abdomen.

Materials.—Nine specimens (5 males and 4 females). A new record for Trinidad.

Range.—Guianas to Argentina and Bolivia.

LEUCOTMEMIS Butler

Leucotmemis differs from *Chrostosoma* in having vein R_1 of the forewing rising from the cell rather than stalked on R_2 - R_5 . Vein Cu_1 of the forewing from close to angle of the cell.

Leucotmemis nexa (Herrick-Schaffer)

Loemocharis nexa Herrick-Schaffer, 1854: f. 254.

Leucotmemis nexa, Hampson, 1898: 224.

Leucotmemis nexa, Draudt in Seitz, 1915: 70, pl. 13a.

Leucotmemis nexa, Kaye & Lamont, 1927: 2.

This species, reported from Trinidad by Kaye & Lamont from St. Ann's, Palmiste and Rock Penal Road, has not been taken at Simla. It is probably improperly placed in *Leucotmemis* as the facies is entirely different from the remainder of the genus with the exception of *L. insperata* (Walker). *L. nexa* resembles a female *Phoenicoprocta vacillans* or a *Calonotus*. It may be separated from the female *vacillans* by having white lateral spots on the first abdominal segment. The sex of *nexa* has never been reported. The facies of *L. insperata* can be encompassed within the range of variation of the female *P. vacillans*. Walker described *insperata* from one female collected at Para, Brazil. There does not appear to be any distinctive venational difference between *Phoenicoprocta* and *Leucotmemis*, though most likely the accessory cell between vein R_2 and vein R_{3+4+5} of the forewing in *Phoenicoprocta* is sufficient to separate the genera. In the only female of *Leucotmemis* I have seen, *L. lemoulti* (Rothschild), the antennal pectinations are equal on both sides of the antennal shaft, whereas in *Phoenicoprocta* and *Calonotus* the antennal pectinations in the female are much longer on the outside of the antennal shaft than on the inside. In addition, *Calonotus* has vein R_2 of the forewing rising from the cell as well as vein R_1 . *Calonotus hoffmannsi* Rothschild, which was removed to *Leucotmemis* by Hampson (1914), is a synonym of *Phoenicoprocta vacillans*. Rothschild similarly described *lemoulti* in *Calonotus*.

Range.—Mexico to Brazil.

NYRIDELA Lucas

A genus containing only two species, which may be distinguished from related forms by their large size. Vein R_1 of the forewing rises from the cell and Cu_2 from near the angle of cell.

Nyridela chalciope (Hubner)

Isanthrene chalciope Hubner, 1827: 20, figs. 469, 470.

Glaucopis acroxantha Perty, 1834: 156, pl. 31, fig. 4.

Nyridela chalciope, Hampson, 1898: 218.

Nyridela chalciope, Draudt in Seitz, 1915: 69,
pl. 9k.

Nyridela chalciope, Kaye & Lamont, 1927, 2.

A large hyaline-winged species with black margins and a black band running from the middle of the costal margin of the forewing to the anal angle. Antennae with yellow tips and the abdomen black with iridescent bluish-green spots.

We have not collected this species at Simla but Kaye & Lamont report it from St. Ann's Valley in the western part of the Northern Range. This species is the South American counterpart of the closely related species from Central America, *Nyridela xanthocera* (Walker).

Range.—Colombia and Brazil.

COSMOSOMA Hubner

A large, somewhat confused, genus that needs revision. Many of the species that Hampson (1898) originally included he subsequently (1914) placed in the genus *Gymnelia* which has a lobed hindwing. Eight species are recorded from Trinidad, of which we record six species.

- | | |
|-------------------------------|---|
| 1. Discal bar broad | 2 |
| Discal bar narrow | 4 |

2. Tegulae and patagia bright red

rubriscapulae

- Tegulae and patagia brown or blue.... 3

3. Abdomen with scarlet subdorsal streaks on first segment *melathoracia*
Abdomen without scarlet subdorsal streaks on first segment *subflamma*

- | | |
|---------------------------------------|---|
| 4. Antennae with white tips | 5 |
| Antennae without white tips | 7 |

5. Costal margin and terminal band of forewing immaculate black *anoxanthia*
Patches of orange-red along costal margin and terminal band at tornus of forewing 6

6. Abdomen with a dorsal red stripe .*achemon*
Abdomen without a dorsal red stripe

remotum

7. Abdomen concolorous orange-yellow

klagesi

Abdomen yellow, second and third segments black with lateral blue spots. *pytna*

Cosmosoma rubriscapulae Kaye
(Pl. III, fig. 11.)

Cosmosoma rubriscapulae Kaye, 1901: 116.

Cosmosoma rubriscapulae, Hampson, 1914:
156.

Cosmosoma rubriscapulae, Draudt in Seitz,
1915: 71, fig. 13b.

Cosmosoma rubriscapulae, Kaye & Lamont,
1924: 3.

The large size combined with the scarlet pagania and tegulae renders this moth distinctive in Trinidad from other *Cosmosoma* species. We have collected three males and three females of this species at Simla. In our specimens the discal bar of the forewings of the females is broader and heavier than in the males.

Range.—Reported only from Trinidad.

Cosmosoma subflamma subflamma (Walker)
(Pl. III, fig. 12)

Glaucopis subflamma Walker, 1854: 159.

Laemocharis panopes Herrich-Schaffer, 1854:
243.

Cosmosoma subflamma, Hampson, 1898: 227.

Cosmosoma subflammum, Draudt in Seitz,
1915: 71, fig. 13b.

Cosmosoma subflamma, Kaye & Lamont, 1924:
3.

The bright red legs distinguish this species from other *Cosmosoma* species in Trinidad. Schaus described a species, *lucia*, from St. Lucia, B.W.I., which Hampson (1898) records as a subspecies of *subflamma* in which the legs are largely black.

Material.—We have taken only one male. Another specimen was taken by F. W. Urich in 1918 in the Arima Valley and Lamont captured a specimen on May 28, 1921, at Palmiste.

Range.—St. Lucia to south Brazil on the eastern side of South America.

Cosmosoma melathoracia Kaye
(Pl. III, fig. 13)

Cosmosoma melathoracia Kaye, 1901: 115, pl. V, fig. 10.

Cosmosoma melathoracia, Hampson, 1914: 157.

Cosmosoma melathoracia, Draudt in Seitz,
1915: 73, fig. 13e.

Cosmosoma melathoracia, Kaye & Lamont,
1924: 3.

Male with dorsal line of iridescent blue scales and a brown valve at base of abdomen edged laterally with white.

Material.—Six males.

Range.—Described and reported only from Trinidad.

Cosmosoma anoxanthia Druce
(Pl. III, fig. 14)

- Cosmosoma anoxanthia* Druce, 1905: 460.
Cosmosoma bolivarensis Klages, 1906: 536.
Cosmosoma anoxanthia, Hampson, 1914: 165,
 pl. VIII, fig. 25.
Cosmosoma anoxanthium, Draudt in Seitz,
 1914: 80, fig. 27m.
Cosmosoma achemon, f. *bolivarensis*, Draudt
 in Seitz, 1914: 79.
Cosmosoma anoxanthia, Kaye & Lamont,
 1924: 3.

Female similar to male except that on the forewing the oblique quadrate patch of blackish-brown scales from the lower extremity of the discal cell to tornus (between veins Cu_1 and Cu_2) is absent in the female.

Material.—Six males and three females.

Range.—Trinidad, Venezuela and Bolivia.

Cosmosoma achemon (Fabricius)
(Pl. III, fig. 15)

- Zygaena achemon* Fabricius, 1781: 162.
Euchromia tyrrhene Hubner, 1827: 23, figs.
 483-484.
Cosmosoma voltumna Druce, 1897: 303.
Cosmosoma achemon, Hampson, 1898: 247.
Cosmosoma achemon, ab. *tyrrhene*, Hampson,
 1914: 527.
Cosmosoma perfenestratum Dyar, 1899: 175.
Cosmosoma achemon, Draudt in Seitz, 1914:
 79, fig. 14c.
Cosmosoma perfenestratum, Draudt in Seitz,
 1914: 80, 1917: 201.

The very bright red dorsal abdominal stripe will separate this species from all other Trinidad *Cosmosoma*. A new record for Trinidad.

Material.—One male from St. Augustine, Trinidad.

Range.—Jamaica, Haiti, Venezuela and Brazil.

Cosmosoma remota (Walker)

- Glaucopsis remota* Walker, 1854: 170.
Cosmosoma remotum, Hampson, 1898: 248,
 pl. IX, fig. 22.
Cosmosoma remotum, Draudt in Seitz, 1914:
 80, fig. 14c.
Cosmosoma remota, Kaye & Lamont, 1924: 3.

Reported by Kaye & Lamont from Tobago. This species is very close to *achemon*, from which it may be distinguished by the absence of the red abdominal dorsal stripe. We have not

taken this species in the Arima Valley but Kaye has specimens from Trinidad in his collection.

Range.—Trinidad, Tobago and Venezuela.

Cosmosoma klagesi Rothschild
(Pl. III, fig. 16)

- Cosmosoma klagesi* Rothschild, 1910: 509.
Cosmosoma klagesi, Rothschild, 1913: 470, pl.
 XIII, fig. 11.
Cosmosoma klagesi, Hampson, 1914: 170.
Cosmosoma klagesi, Draudt in Seitz, 1914: 82,
 fig. 14g.
Cosmosoma klagesi, Kaye & Lamont, 1924: 4.

Material.—Fifty-one males and twenty females. Our commonest *Cosmosoma* in the Arima Valley.

Range.—Trinidad and Brazil.

Cosmosoma pytna Druce

- Cosmosoma pytna* Druce, 1906: 78.
Cosmosoma pytna, Hampson, 1914: 157, pl.
 VIII, fig. 12.
Cosmosoma pytna, Draudt in Seitz, 1914: 83,
 fig. 27m.
Cosmosoma pytna, Kaye & Lamont, 1924: 4.

We have not collected this species in the Arima Valley nor, insofar as the literature reveals, has it been collected since the holotype was taken in Trinidad.

DIXOPHLEBIA Butler

The fringes of hair along the lower radial, median and cubital veins of the forewing will distinguish this genus from other genera of Ctenuchidae.

Dixophlebia holophaea Hampson
(Pl. III, fig. 17)

- Dixophlebia holophaea* Hampson, 1909: 346.
Dixophlebia holophaea, Hampson, 1914: 174,
 pl. IX, fig. 9.
Dixophlebia holophaea, Draudt in Seitz, 1914:
 85, fig. 14k.

A grayish-black moth with hyaline in the discal cell areas in both wings.

Material.—Two males.

Range.—Surinam and British Guiana. A new record for Trinidad.

PSEUDOMYA Hubner

A genus probably derived from *Saurita*, from which *Pseudomya* may be distinguished by having the hind tarsal joints fringed with scales in the males.

Pseudomya melanthus (Stoll)
(Pl. III, figs. 18, 19)

Sphinx melanthus Stoll, 1782: pl. 367, C.

Pseudomya melanthus, Hampson not Stoll, 1898: 264. (*trigutta* Walker).

Pseudomya melanthus, Hampson, 1914: 175.

Pseudomya melanthus, Draudt in Seitz, not Stoll, 1914: 87, fig. 14m. (*trigutta* Walker).

Pseudomya melanthus, Draudt in Seitz, 1917: 202.

Pseudomya melanthus, Kaye & Lamont, 1927: 4.

The facies of this species is very similar to *Pseudomya sanguiceps* Hampson from Panama (Hampson, 1898: 264, pl. X, fig. 4) figured in Seitz on line 14m. The medial black band of the forewings is darker and wider than shown in the Seitz figure and extends from the costal to the inner margin in the male. Our single female, while having a very distinct quadrate patch of dark scales at the discal veins, has only a scattering of scales below the cell. Length of forewing of the male 10 mm. and of the female 11 mm.

Material.—One male and one female.

Range.—Trinidad and Surinam.

RHYNCHOPYGA Felder

Differs from *Saurita* and *Pseudomya* in having Cu₁ and M₃ on a long stalk in the hindwing.

Rhynchopyga flavicollis (Druce)
(Pl. III, fig. 20)

Amycles flavicollis Druce, 1884: 46, pl. 7, fig. 11.

Rhynchopyga flavicollis, Hampson, 1898: 270.

Rhynchopyga flavicollis, Draudt in Seitz, 1914: 90, fig. 15e.

The long, very narrow brown wings of this slender, small species is distinctive. Our single male specimen lacks the orange streak on the patagia present on the holotype. Our specimen also has less orange on the tegulae.

Material.—One male. A new record for Trinidad.

Range.—Guatemala, British Honduras, Costa Rica, Panama and Colombia.

SAURITA Herrick-Schaffer

Probably not a natural genus but attempts to divide it have thus far been unsuccessful. Veins M₃ and Cu₁ of the hindwing arise from the same point or are very shortly stalked.

1. Abdomen of male with ventral valve covering basal segments. Abdomen of male and

female large, with iridescent blue sublateral spots and crimson anal tufts. . . . *cassandra*
Abdomen of male with no ventral valve.

Abdomen of male and female otherwise 2

2. Thorax with crimson patches only. 3

Thorax orange red or crimson 6

3. Abdomen with whitish patches 4

Abdomen with brown or black patches. 5

4. Discal cell of forewing brown-scaled

lacteata

Discal cell of forewing hyaline. . . *arimensis*

5. Forewing uniformly hyaline or smoky hyaline *perspicua*

Forewing with post-discal milky hyaline band *clusia*

6. Vertex of head crimson red. *salta*

Vertex of head black 7

7. Wings fully scaled with only slight thinning of scales between veins *conclisa*

Discal cell and area below discal cell of forewing hyaline 8

8. Underside of body yellow *temenus*

Underside of body black *afflicta*

Saurita cassandra (Linnaeus)
(Pl. III, fig. 21)

Sphinx cassandra Linnaeus, 1758: 494.

Saurita cassandra, Hampson, 1898: 274, fig. 127.

Saurita cassandra, Draudt in Seitz, 1915: 93, fig. 15f.

Saurita cassandra, Kaye & Lamont, 1927: 4.

A robust, brown-winged *Saurita* with the discoidal patch darker and extending somewhat along the cubital veins. Males and females similar except for the longer pectinations on the male antennae.

Material.—One male.

Range.—Venezuela to Argentina.

Saurita clusia (Druce)
(Pl. III, figs. 22, 23)

Laemocharis clusia Druce, 1897: 303.

Hypocharis clusia, Hampson, 1898: 271, fig. 125.

Hypocharis clusia, Draudt in Seitz, 1915: 91, fig. 15e.

Hypocharis clusia, Kaye & Lamont, 1927: 4.

Saurita clusia, Forbes, 1939: 121.

Forbes (1939: 121) placed *clusia* in *Saurita*, pointing out that the character Hampson (1898: 271) employed to erect the genus *Hypocharis* is equally true of *Saurita*, namely, vein M₁ of

the forewing is more or less from below the angle of the cell in all species of *Saurita* as well as Hampson's *Hypocharis*.

This species will key to *Saurita nox* (Druce) in Hampson's key (1898: 275). Hampson's footnote indicates that he examined the holotype of *nox* which was in the Staudinger collection. In his description of the species he mentions "a broad diffused whitish band from just beyond middle to termen." He gives the wing expanse as 22 mm.

Druce, on the other hand, neither in his original description (1896: 30) nor in the *Biologia* (1897: 341, pl. 71, fig. 11) where he copies his original description, makes any mention of a whitish postmedian band but states simply, "primaries and secondaries smoky hyaline, with the veins all black." His figure (*l.c.*) illustrates a smoky hyaline-winged moth with blackish veins. Druce records the wing expanse as 1¼ inches.

Draudt in Seitz (1915: 93, fig. 15g) shows a figure resembling the figure of Druce. Forbes conjectures that Draudt's figure is of *S. fumosa*. In his description, however, Draudt writes of a "postdiscal, faded, whitish spot." He gives the wing expanse as 22 mm. He compares the species to *Saurita lacteata* Butler which has a different-shaped inner margin of the hindwing. (See Forbes, *l.c.* for grouping of species of *Saurita*).

Hampson (1914: 186) synonymizes *Chrostosoma maratha* Druce as the female of *Saurita nox*. The holotype is in poor condition with the wings torn and rubbed and the abdomen missing. However, the whitish postdiscal band crosses the forewing in the photograph slightly distad of the discoidal veins. The facies of the forewing looks very similar to that of *clusia*.

Specimens from Trinidad are included within the series of *Saurita clusia* in the British Museum (Natural History) collection. These Trinidad specimens and also those in Kaye's private collection under *clusia* are similar to the specimens we collected. However, if I were to follow my interpretation of Forbes (1939: 121) I should have identified them as *nox*. Forbes states that *clusia* is smaller than *nox*, the white postmedian band narrower sex for sex, and the blue spotting is distinctive, and for *nox*, "There are no blue spots; in the male the white area invades the outer third or half the cell, in the female the extreme apex of the cell may be pale." First of all, our series of specimens varies from having a distinctively blue spotted abdomen to a completely unspotted concolorously colored abdomen with the completely unspotted section

representing approximately half the collection. Our specimens are much larger than the specimens in the American Museum of Natural History from Panama identified as *clusia* by Forbes. All of our specimens have the postmedian band invading the discal cell to the extent of half or more. Lastly, our specimens differ in genitalia from those in the American Museum under *clusia*.

Hampson (1898: 271) mentions the blue spotting in regard to *clusia*. His figure of *clusia* is similar to our photograph of the holotype of *clusia*, but his wing expanse is much larger (30 mm.) (and Druce 1¼") than the six specimens named *clusia* by Forbes (23-25 mm.) in the American Museum of Natural History. In other than the size difference, Hampson and Forbes agree.

Aside from the discrepancy between Druce's original description of *nox* and the subsequent descriptions by other authors which make the identity of *nox* questionable, it is quite possible that we are concerned with more than two species. However, I consider that it would be unwise to describe the Trinidad form without having material throughout the range of the above two species.

Saurita lacteata (Butler)

Dycladia lacteata Butler, 1877: 34, pl. 17, fig. 3.

Saurita lacteata, Hampson, 1898: 276, fig. 128.

Saurita lacteata, Draudt in Seitz, 1915: 93, fig. 15g.

Saurita lacteata, Kaye & Lamont, 1927: 4.

This species is listed by Kaye & Lamont as occurring in Trinidad but the specimens in Kaye's collection under this name are similar to the following new species. The specimens under *lacteata* in the British Museum (Natural History) from Trinidad are likewise in agreement with the following species. Butler describes *lacteata* from the Rio Jutahi, Amazons.

Saurita arimensis, new species (Pl. I, fig. 3; Pl. II, fig. 3)

Length of forewing of male 10.5-11.5 mm.

Related to *Saurita lacteata* Butler from which *arimensis* differs in having the discal cell hyaline and in not having a yellowish-white patch below the cell and another yellowish-white patch beyond the cell.

Antennae bipectinate in the male with each pectination dilated and bristled on the distal end. Palpi brown, reaching vertex of head with fan-shaped brown tuft on first segment. Whole head uniform brown.

Patagia and disc of thorax uniform brown with a small white patch on the mid-dorsum of the metathorax. Tegulae brown with a crimson patch on anterior margin near patagia (shoulders) and a white bar at discal edge of tegulae on the anterior margin of forewing. The inner half of tegulae along the disc of the thorax crimson.

Some white on the outer edge of the basal half of the forecoxae on the episternum (2nd). The remainder of the legs and the lateral and ventral parts of the thorax brown.

Fore- and hindwings hyaline. Veins brown. The forewings narrowly bordered with brown but the apex of the wings broadly brown. The brown patch at the apex extending within the wing to the point where veins R_4 and R_5 fork. A relatively broad brown discal bar (1.25 mm.). Hindwings with narrow brown margins broadening at apex. At the 1st anal fold the brown color extends within the wing for approximately one-third of the length of the wing from the margin, and a brown patch extending into the wing at the anal angle for approximately the same distance.

Abdomen with the dorsum of the first and second segments and to a variable extent the third segment creamy white. The bullae creamy white. A creamy white band extends from bullae along the spiracular region of the abdomen for four segments. The band is broadest at the base and narrows toward the distal end of the abdomen. The remainder of the abdomen brown.

The name *arimensis* has been taken from the type locality, Arima Valley.

Material.—All types were taken at Simla, Arima Valley, Trinidad. Holotype, male, Catalog No. 57200, 2-V; 6 paratypes, (57201) 2-VI, (57202) 16-III, (57203) 21-IV, (57204) 13-II, (57205) 7-I, (57206) 3-VI.

Disposition of type material.—The Department of Tropical Research, New York Zoological Society, will retain two paratypes, Catalog Nos. 57205 and 57206. Paratype, Catalog No. 57204, is in the collection of the British Museum (Natural History) and paratype, Catalog No. 57203, is in the United States National Museum collection. The holotype, Catalog No. 57200, and the paratypes, Catalog Nos. 57201 and 57202, are in the American Museum of Natural History.

Saurita perspicua Schaus

Saurita perspicua Schaus, 1905: 187.

Saurita perspicua, Hampson, 1914: 185, pl. IX, fig. 31.

Saurita perspicua, Draudt in Seitz, 1915: 93, fig. 28e.

Saurita perspicua, Kaye & Lamont, 1927: 4.

This species has not been collected since the original type. Subsequent mention in the literature has been based on the original description. The type is a female in the U.S. National Museum. Schaus (1905) states that the wings are smoky hyaline and Hampson (1914) simply says that they are hyaline. We have not taken this species at Simla.

Range.—Trinidad.

Saurita salta (Schaus)

Thrinacia salta Schaus, 1894: 226.

Saurita salta, Hampson, 1898: 277, pl. X, fig. 12.

Saurita salta, Draudt in Seitz, 1915: 94, fig. 15h.

Saurita salta, Kaye & Lamont, 1927: 5.

Range.—Described from Venezuela. Kaye & Lamont report it from Trinidad, with no data.

Saurita temenus (Stoll)

Sphinx temenus Stoll, 1781: pl. 367, D.

Saurita temenus, Hampson, 1898: 279.

Saurita temenus, Draudt in Seitz, 1915: 94, fig. 16b.

Saurita temenus, Kaye & Lamont, 1927: 5.

See following species, *Saurita afflicta*, for discussion.

Range.—Surinam, Amazons.

Saurita afflicta (Walker)

(Pl. III, figs. 24, 25)

Glaucopis (Pseudomya) afflicta Walker, 1854: 144.

Glaucopis afflicta, Butler, 1877: 29, pl. 7, fig. 12.

Saurita temenus, Hampson, 1898: 279 (in part).

Saurita venezuelensis Klages, 1906: 538.

Saurita venezuelensis, Draudt in Seitz, 1917: 94, fig. 15h.

Saurita temenus, Draudt in Seitz, 1917: 94, fig. 16b (in part).

Saurita afflicta, Forbes, 1939: 123.

The *Saurita temenus* record of Kaye & Lamont (1927: 5) may be in error and their specimens rightfully placed in this species. The specimens we have taken at Simla are *S. afflicta*. This species was listed by Hampson (1898: 279) as a synonym of *S. temenus* and subsequent authors until Forbes (1939: 123) followed Hampson. Forbes was the first to point out that the two names represented different species most easily separated by the yellow ventrum of *S. temenus* and the blackish ventrum of *S. afflicta*.

However, since *S. afflicta* was described from the Amazons and *S. temenus* from Surinam, it is possible that both species inhabit Trinidad.

The females may be distinguished from the males by having the spaces between the veins beyond the cell hyaline.

Material.—17 specimens: 12 males and five females.

Range.—Honduras to the Amazons.

Saurita concisa (Walker)

Euchromia concisa Walker, 1854: 243.

Thrinacia afflicta Druce, 1884: 56 (not Walker).

Saurita concisa, Hampson, 1898: 279.

Saurita thoracica Klages, 1906: 538.

Saurita concisa, Hampson, 1914: 189.

Saurita thoracica, Draudt in Seitz, 1915: 94.

Saurita concisa, Kaye & Lamont, 1927: 5.

Kaye & Lamont placed *Saurita venezuelensis* Klages as a synonym, but I have followed Forbes and synonymized *venezuelensis* under *Saurita afflicta* Walker.

Kaye & Lamont record this species from Palmiste, Trinidad, but we have not collected it as yet at Simla.

Range.—Panama to the Amazons.

PSOLOPTERA Butler

A small genus closely related to *Saurita*, from which it differs by having vein R_1 forked with R_2 in the forewing.

Psoloptera leucosticta (Hubner)

Glaucoptis leucosticta Hubner, 1827: t. 162.

Psoloptera leucosticta, Hampson, 1898: 285.

Psoloptera leucosticta, Draudt in Seitz, 1915: 96, fig. 15 m.

Psoloptera leucosticta, Kaye & Lamont, 1927: 5.

Kaye & Lamont report this species from Trinidad, one specimen from Guaico at the southern foot of the Northern Range and two specimens from Palmiste. We have not taken it at Simla, but we collected the species at Caripito, Venezuela, across the Gulf of Paria from Trinidad. The wings and body are purplish-black with two white points at the base of the abdomen.

Range.—Venezuela, Trinidad, Guianas and Amazons.

DYCLADIA Felder

A small genus of moths that are very beetle-like. The following species in particular, like the

species of the genus *Correbidia* in the next subfamily, resemble a Lycidae beetle.

1. Orange lateral line of the abdomen not reaching beyond middle of the abdomen and no black spot at the base of the forewing *correbioides*

Orange lateral line of the abdomen absent only on the last segment and base of forewing with large black spot. . . *basimacula*

Dycladia correbioides Felder

Dycladia correbioides Felder, 1874: pl. 102, fig. 20.

Dycladia correbioides, Hampson, 1898: 293, fig. 139.

Dycladia correbioides, Draudt in Seitz, 1915: 99, fig. 16d.

Dycladia correbioides, Kaye & Lamont, 1927: 5.

Kaye & Lamont record this species from Palmiste but see following species, *Dycladia basimacula* Schaus.

Dycladia basimacula Schaus
(Pl. III, fig. 26)

Dycladia basimacula Schaus, 1920: 9.

It is most likely that the *D. correbioides* of Kaye & Lamont is this species. *D. correbioides* is the name used for the form found in Colombia and Panama, and *D. emerita* for the form from Costa Rica to Mexico. Schaus described *D. basimacula* from Venezuelan and Trinidad material.

Material.—Four males.

Range.—Trinidad and Venezuela.

SYNTOMEIDA Harris

The three posterior veins from the discal cell of the hindwing are forked.

Syntomeida melanthus (Cramer)

Sphinx melanthus Cramer, 1779: pl. 248, C.

Sphinx nycteus Stoll, 1780: pl. 325, F.

Euchromia apricans Walker, 1854: 224.

Syntomeida albifasciata Butler, 1876: 366.

Syntomeida melanthus, Hampson, 1898: 306, fig. 138.

The lustrous blue-black wings with a variable number of quadrate yellow spots and orange-red and black bands on the abdomen separate this insect from other Trinidad ctenuchids. The names *albifasciata*, *nexilis* and *nycteus* apply to variants in either the number of yellow wing spots or abdominal coloration.

Kaye & Lamont report this species from San Fernando.

Range.—Mexico to Uruguay and Peru.

HISTIAEA Walker

The largest of the Trinidad ctenuchids, with densely scaled, brown wings variously marked with red and yellow or grayish spots.

1. Abdomen with two basal segments completely yellow dorsally. Forewing with extensive longitudinal red rays running from base *meldolae*
Dorsum of abdomen brown with two subdorsal spots on basal segment, and triangular, subdorsal yellow spots on the anterior parts of the following two segments. Forewing with at most red or reddish-tinged spots or small streaks..... *cephus*

Histiaea meldolae Butler (Pl. III, fig. 27)

Histiaea meldolae Butler, 1876: 362.

Histiaea meldolae, Druce, 1884: 42, pl. 6, fig. 14.

Histiaea meldolae, Hampson, 1898: 311.

Histiaea meldolae, Draudt in Seitz, 1915: 101, fig. 16g.

Histiaea meldolae, Kaye & Lamont, 1927: 5.

Material.—Three males and three females.

Range.—The holotype is a Trinidad specimen. British Guiana, Venezuela, and Panama.

Histiaea cepheus (Cramer) (Pl. III, fig. 28)

Histiaea cepheus Cramer, 1780: pl. 109, E.

Histiaea cepheus, Hampson, 1898: 313.

Histiaea monticola Klages, 1906: 538.

Histiaea monticola, Hampson, 1914: 203.

Histiaea cepheus, Draudt in Seitz, 1915: 101, fig. 16g.

Histiaea monticola, Draudt in Seitz, 1915: 102.

Histiaea cepheus, Kaye & Lamont, 1927: 6.

Material.—Forty-six males and 17 females.

Range.—Venezuela to Surinam.

MACROCNEME Hubner

This genus of iridescent wasp-like moths is in a very confused condition. The iridescence of the wings, while diagnostic in many instances, is extremely difficult to describe. Forbes (1939) has written the only paper that is of any real assistance. The descriptions in Hampson (1898 and 1914) are valuable but his taxonomic treatment is inadequate. Genitalic studies of the types and series of specimens must be made and associated with other characters before

identification in this genus will have any reliability.

The following key is based on specimens we have collected and some unidentified Trinidad material loaned by the British Museum (Natural History).

1. First segment of abdomen with four white spots; two subdorsal and two lateral. No ventral valve in male. Large species with a wing length of 16 mm. or more..... 2
First segment of abdomen with only two iridescent blue or green subdorsal spots on conspicuous abdominal bullae. Ventral valve present in male. Smallest species with a wing length of 14 mm. or less 6
2. Males 3
Females 5
3. At least the basal $\frac{2}{3}$ of the ventrum of the abdomen with a broad uninterrupted white band *thyra*
Otherwise; white of underside of the abdomen broken up into spots..... 4
4. Forecoxae iridescent blue..... species?
Forecoxae white *spinivalva*
5. Iridescence of the forewing uniform green to end of discal cell except slight black along base of costal margin and small black point on the base of the anal vein. (True of males also) *thyra*
Iridescence of forewing interrupted by a black band from inner margin to at least the anterior part of discal cell. (True of males also) *spinivalva*
6. Forewing with streaks of iridescent blue or green from base of wing to end of discal cell *vittata*
Forewing with only blue or green spots at base of wing 7
7. Abdomen with subventral white spots on two medial segments *plumbea*
Abdomen without subventral white spots *albitarsia*

Macrocneme plumbea (Hampson), new combination (Pl. III, fig. 29)

Poliopastea plumbea Hampson, 1898: 337, pl. XII, fig. 26.

Poliopastea plumbea, Draudt in Seitz, 1915: 110, fig. 18b.

Our specimens agree with Hampson's original description of *plumbea* but the description is inadequate for proper determination. Hampson states that the abdominal valve is blue edged

with white, with a white patch behind it. Our specimens have these characters, but in addition the two segments caudad of the white patch have small subventral white spots. Draudt in Seitz may have had similar specimens, as he states: "—the next rings indistinct, white sublateral spots." Kenedy, in notes, writes that the type has small, sublateral spots on the next segment and sublateral metallic blue spots on next two segments. One of our specimens shows only faint traces of the second pair of spots. All of our specimens have subventral blue spots on the subterminal abdominal segments but they may be very faint. The hind legs are missing on the holotype, but in the series of specimens of *plumbea* (not type material) in the British Museum (Natural History) the hind tarsi are white. Hampson's male holotype came from the lower Amazons, Paratins. Draudt records the species from the Amazon and French Guiana, and specimens in the British Museum (Natural History) collection are from Trinidad, Venezuela, British Guiana and Sao Paulo, Brazil. My identification of the Trinidad material is provisional on a genitalic examination of the holotype in the British Museum.

Hampson erected a new genus, *Poliopastea*, for *plumbea* and made *plumbea* the type species of the genus. Hampson's conception of the differences between *Macrocneme* and *Poliopastea* appears to be the correct palpi in *Poliopastea*, veins Cu₁, M₃ and M₂ of the forewing close to the angle of the cell and vein R₂ of the forewing from the cell. The specimens that I have seen from Trinidad have individuals with both correct and upturned palpi. Vein Cu₁ of the forewing is variable in *Macrocneme* so that the character, veins Cu₁, M₃ and M₂ from close to angle of cell, has no significance and some species of *Macrocneme* have vein R₂ of the forewing from the cell. Consequently, I consider *Poliopastea* a synonym of *Macrocneme*. I have not examined any of the other species that have been placed in *Poliopastea* but it seems likely that *obscura* (Wallengren) and *viridis* (Druce) can be included in *Macrocneme*. Hampson (1914: 207) placed *ochendeni* Rothschild in *Macrocneme*. He erected a new genus *Pseudophaio* for *rosenbergi* Rothschild and provisionally transferred *verdivittata* to *Calonotus*. *Poliopastea pava* (Dognin) was aberrant in the genus and required a separate section. It was originally described by Dognin in the genus *Thysanopryana*, which is a synonym of *Baritius* in the family Arctiidae.

Kaye & Lamont listed *plumbea* as a synonym of *eacus* along with *vittata* and *nigritarsia*. The figure of *eacus* in Stoll (1781, fig. 335 C) has

evanescent, iridescent blue in the cell and somewhat beyond, and *vittata* (see above under *vittata*) has iridescent blue above and below the cell as well as within the cell. Hampson's *nigritarsia* is a larger moth than *eacus* and the iridescent blue is more distinct and extensive. Lamont & Callan (1950: 197) report *albitarsia* from Trinidad (Palmiste). This species may be separated from *plumbea* by the absence of the white spots on the ventrum of the abdomen. Both *eacus* and *nigritarsia* have black hind tarsi, whereas *albitarsia*, *plumbea* and *vittata* have the terminal segments of the hind tarsi white.

Material.—Four males from Simla and two males from the British Museum (Natural History) from Caparo and San Fernando, Trinidad.

Macrocneme thyra thyra Moschler

Macrocneme thyra Moschler, 1883: 334, 1. 18, fig. 24.

Macrocneme thyra, Hampson, 1898, 321.

Macrocneme thyra, Draudt in Seitz, 1915, 103, fig. 17a.

Macrocneme albiventer Dognin, 1923: 2.

Macrocneme thyra, Kaye & Lamont, 1927: 6.

Macrocneme thyra, Forbes, 1939: 129, 1. 1, fig. 3 (genitalia).

This is the nomenclatural type that was described from Surinam. One male specimen from the collection in the British Museum (Natural History) I have tentatively assigned to this form. It was collected at Tabaquite, Nariva District, Trinidad. This single specimen has a very short streak of iridescent blue at the base of the wing in the lower part of the cell and just below the cell. Iridescent blue in the distal half of the cell, just above the cell and below the anal vein, the latter extending almost to the base of the wing. The area between the cell and the anal vein black but with a trace of iridescence below the iridescence in the cell end. This specimen has more extensive black in the basal part of the wing than Hampson indicates for *thyra*. The ventrum of the abdomen is white. While I have not removed the genitalia, it is well extruded and I have been unable to see any significant difference between the genitalia of this specimen and the genitalia of *thyra* that Forbes (1939) figures, and the following race.

Range.—Guianas, Brazil, Peru to Panama?

Macrocneme thyra intacta Draudt (Pl. III, fig. 31)

Macrocneme thyra, subspecies 1, Hampson, 1898: 321.

Macrocneme thyra intacta, Draudt in Seitz, 1915: 103.

I am unable to find any essential details of the genitalia of the Trinidad specimens different from the genitalic figures of Forbes (1939). Both processes of the male valves are curved as in the figure and the upper process of the left valve has a distinct tooth on the inner edge. This last feature is not shown in the figure but stated in the text. The juxta is squarely cut off and short. The uncus is the same shape as in the figure, but with small, narrow, lateral-winged margins which I do not see in the figure.

This is subspecies 1 of Hampson. Draudt appears to have given the subspecies a name on the basis of Hampson's description without having specimens before him. Hampson (1898) characterized it in part by stating "Forewing with blue-green at base entire." This is true of our Trinidad specimens except as noted in the key; namely, the Trinidad specimens have black on the base of the costal margin and a small black streak or spot on or near the base of the anal vein. This last-mentioned black streak or spot is never very conspicuous and is occasionally absent.

Material.—144 specimens from Simla (137 males and 7 females) and 9 specimens (6 males and 3 females) from Port of Spain, Guaico, Ariapite Valley and St. Ann's borrowed from the British Museum (Natural History).

Range.—Stated by Hampson as Trinidad and Colombia.

Macrocneme spinivalva, new species
(Pl. I, fig. 4; Pl. II, fig. 4)

Length of forewing of male 17 mm., of female 18 mm.

Antennae dark brown, bipectinate. Each pectination tufted on distal end and length of pectinations rapidly decreasing at proximal and distal ends of antennal shaft. Pectinations shorter in male than in female.

Palpi upturned to vertex of head. First segment of palpi clothed with ragged, dark brown scales with an immaculate white medial tuft of broad scales on anterior face, for two-thirds to three-quarters the length of the second segment of the palpi from the proximal end. The line of white scales absent in female. Ground color of second and third palpal segments dark brown in both sexes.

Front of head dark brown with two white spots on upper edge beneath the antennal scapes in both sexes. Vertex of head brown.

Patagia (collar) with a pair of dorsal white spots and a pair of subdorsal white spots. In the male, but not the female, each dorsal spot joined to its respective subdorsal spot by a fine line of white scales on the anterior margin of

the patagia. Immediately below the subdorsal spots and hardly separated from them, anterior to the bases of the tegulae and approximately in line with the middle of the eyes, a small white spot. A rectilinear episternal white spot in line with the lower part of the eyes and base of palpi. The episternal spot is present in the female though usually smaller than in the male, but the spot below the subdorsal spot is absent in the female. Tegulae dark brown with iridescent green reflections most pronounced on the anterior edge. Dorsum of thorax dark brown with iridescent reflections in various lights, most distinct on the metathorax.

Forecoxae of the male white but the remainder of the forelegs brown with faint iridescent reflections except for the caudal edge of the femur of the forelegs which is gray. Each of the forecoxae of the female with two small white spots on the proximal end, one laterad and one dorsad. The remainder of the female legs brown with varying iridescent reflections. Mesothoracic legs in both sexes brown with some blue reflections, with a small white spot on the distal end of the femur. Metathoracic legs of the same brown color with reflections but with the distal one-half to two-thirds of the tibia in both sexes fringed. The metatarsus with long fringe. The fringe on the third, fourth and fifth tarsal segments white.

Forewing with two white spots on base of wing near tegulae. Distinct blue iridescence in the forewing is confined to the following five areas:

- (1) A streak the length of the discal cell above the discal cell,
- (2) to the distal half of the discal cell,
- (3) to the same respective part of the wing below the discal cell except that the iridescence follows vein Cu_2 in the direction of the tornus a little beyond the end of the discal cell,
- (4) a basal patch below the base of the discal cell, and
- (5) a median streak below the anal vein.

The remainder of the wings including the veins through the iridescent areas blue to brownish-black depending on the age of the specimen. The above description of the forewing pattern may be summarized by saying that the iridescence is confined to the plane of the end of the discal cell interrupted by a dark transverse band perpendicular to a dark anal streak. Underside of forewing with the basal half of the wing to cell end iridescent blue.

Upperside of hindwing bluish or brownish-black depending on the age of the specimen. Underside of hindwing iridescent blue except

for apical and anal area. In old specimens the iridescence may be restricted to the cell and costal area.

Abdomen with two pairs of white spots, one pair subdorsal and the other on the hoods or bullae. First segment of abdomen blackish-brown and the remainder of the abdominal segments iridescent blue-green with bluish-black subdorsal longitudinal bands. The background color may become quite brassy in old specimens. Ventrums of male without a basal ventral valve but a pair of subventral white spots on the first segment in both sexes. Subsequent segments of the abdomen in both sexes with a midventral white spot except the last abdominal segment which, like the first segment, has a pair of white subventral spots.

Male genitalia with base of uncus broadly inflated and the edges thin in cross-section with the distal process normally directed ventrally and slightly spatulate. Valves large with two processes, the dorsal process curved with a distinct thorn-like structure on inner edge of the distal half and a ventral process which is slender and hirsute. Juxta very slender, so slender as to be remarkable for the genus.

Female genitalia with signa of bursa copulatrix spherical, with long spines, sea-urchinlike, with small anterior portion unspined. In the female genitalia of *thyra*, the other species of this section of the genus in Trinidad, the signa is ovoid or almost subquadrangular with short spines.

This is most likely the species mentioned by Forbes (1939: 126, pl. II, fig. 8) which he refers to as *Macrocneme* species. It will run to this species in his key to the species of *Macrocneme* and his figures are extremely similar. The tegumen and uncus are less inflated laterally than in *spinivalva* and do not show any part of the distal end of the uncus. The thorn or tooth on the dorsal process of the valve appears more pronounced and acuminate than in Forbes's figure of the valve, but this may be a matter of perspective.

This species seems to be most closely related to *thyridia* with which we had it confused in our collection. The tooth or thorn-like structure on the upper process of the valve and extremely slender juxta will separate *spinivalva* from *thyridia*. The spined condition of the valve can often be seen without removing the genitalia in the male. Thus far, we have not found *thyridia* in Trinidad.

The specific name *spinivalva*, meaning thorn-valve, refers to the thorn-like structure on the upper process of the male genitalic valve.

Material.—Holotype, male, Catalog No. 5716,

Simla, Arima Valley, 27-III; allotype, female, Catalog No. 5717, Simla, 26-III; paratypes, male and female in coitu, (5718) Simla, 22-XII; paratypes, males, (5719) Simla, 16-II—(5720) #288, Trinidad, B.M.—(5721) June, 1902, Ariapite Valley, B. M.—(5722) June, 1902, Ariapite Valley, Trinidad, B. M.; paratypes, females, (5345) Simla, 17-III—(5724) Simla, 6-III—(5725) Simla, 27-III—(5726) Simla, 13-III—(5727) Trinidad, B. M.—(5728) Trinidad, B. M.—(5729) Trinidad, Dr. Jackson, 1921-1922, B. M.—(5730) Trinidad, A. Hall, Feb. 1930, B. M.—(5731) Ariapite Valley, July, 1902—(5732) Trinidad, B. M.—(5733) Trinidad, B. M.—(5734) Trinidad, F. Shade, Nov. 1920, B. M.—(5735) Trinidad, B. M.—(5736) Trinidad, B. M.

Disposition of type material.—The Department of Tropical Research, New York Zoological Society, retains the two paratypes in coitu (5718). Those paratypes listed above with abbreviation "B.M." are specimens borrowed from the British Museum (Natural History) and have been returned to England. Paratype 5723, female, is in the United States National Museum collection. The holotype, allotype and the remaining paratypes are in the American Museum of Natural History, New York.

Macrocneme vittata Walker
(Pl. III, fig. 30)

Macrocneme vittata Walker, 1854: 249.

Macrocneme vittata, Hampson, 1898: 249, Pl. XII, fig. 23.

Macrocneme nigritarsis, aberration 1, Hampson, 1898: 326.

Macrocneme caurensis Klages, 1906: 540 (after Hampson: 1914: 207).

Macrocneme vittata, Draudt in Seitz: 1915: 105, fig. 17d.

Macrocneme nigritarsis, aberration *trinitatensis*, Strand, 1917: 84.

Macrocneme vittata, Forbes, 1939: 127, 133.

This species has not been reported by Kaye & Lamont. They did, however, list it as a synonym of *eacus* (Stoll). *Macrocneme eacus* does not seem to have been found in Trinidad. It is a small *Macrocneme* with a suffused bright blue forewing in contrast to *vittata* which has definite if variable iridescent blue marks. The latter seems closely related to *alesa* Druce, which differs in having more green than *vittata*. The costal green of *vittata* extends but little beyond the discal cell from the base, whereas in *alesa* it runs to near the termen. The blue streak on the anal vein extends beyond the middle of the wing in *alesa*, but in *vittata* from Trinidad this streak in the

specimen with it most enlarged is still only half the length of the discal cell. This species will key to *alesa* in Hampson (1898: 322) since in the key *vittata* is separated on the basis of having green only in and above the cell, which is contrary to what Hampson states in his description (1898: 325). Forbes (1939: 127) similarly has *vittata* restricted to blue in costal half or less. The amount of blue in our specimens is variable in the anal region of the forewing; from only a spot near the base of the wing to streaks above and below the anal vein reaching to approximately the end of the discal cell, above the anal vein (origin of vein Cu₂) and half the length of the discal cell below the anal vein. The holotype of *alesa* is a female from Bolivia and the holotype of *vittata* from Para, Brazil.

Hampson (1898: 326) on the basis of one female specimen identified as *nigritarsia*, described an aberration from Trinidad distinguished by having white sublateral spots on the four medial segments of the abdomen. Hampson did not mention in his description that this specimen has some white on the tarsi, which has been seen by Kenedy. Later Strand (1917: 84) named this aberration of Hampson *trinitatensis*. Hampson's female specimen can hardly be anything else than a normal *vittata* female, and thus, since the Trinidad locality record for *nigritarsis* appears to be dependent on this single specimen, *nigritarsis* cannot be considered as having been taken in Trinidad.

Material.—Nine specimens (5 males and 4 females). Thirty specimens (14 males and 16 females) in the British Museum (Natural History). One from Caparo, four from Ariapite Valley and the remainder labelled only Trinidad.

Range.—Amazons and Venezuela (*caurensis*).

CALONOTOS Hubner

Key to the Trinidad Species of *Calonotos*

- 1. Wings without hyaline spots. . . *helymus*
Wings with hyaline spots. 2
- 2. Abdomen cupreous with black stripes *tiburtus*
Abdomen iridescent green with black stripes 3
- 3. Basal segment of abdomen black with a pair of subdorsal white spots and lateral hoods white *craneeae*
Basal segments of abdomen green without a pair of white spots, but with dorsal black stripes and lateral white hoods *tripunctatus*

Calonotos helymus (Cramer)

Sphinx helymus Cramer, 1775: I, pl. 2, figs. D, E.

Glaucopis aterrima Sepp, 1848: p. 17, pl. 97.

Calonotos helymus, Hampson, 1898: 335.

Calonotus helymus, Draudt in Seitz, 1915: 109, fig. 18a.

Calonotus helymus, Kaye & Lamont, 1927: 7.

This species was collected at Palmiste by Lamont. We have not collected it in the Arima Valley as yet. Hampson in his key (1898: 333) states, "Wings without hyaline spots," which separates this species from all other *Calonotos* collected to date from Trinidad. Draudt's figure in Seitz (1915: 18a) has a single hyaline spot in the discal cell area of the forewing, although his text states that the wings are unspotted.

Range.—French and British Guiana.

Calonotos tiburtus (Cramer)
(Pl. III, fig. 32)

Sphinx tiburtus Cramer, 1780: pl. 237C.

Calonotos tiburtus, Hampson, 1898: 333, fig. 154.

Calonotus tiburtus, Draudt in Seitz, 1915: 108, figs. 17i ♂ & ♀.

Calonotus tiburtus, Kaye & Lamont, 1927: 6.

The bright, metallic coppery stripes on the abdomen serve to distinguish this species from other *Calonotos* of Trinidad. We have found the species quite common flying in the daytime in forested parts of the Nariva Swamp south of Brigand Hill. Male genitalia with a pair of lobelike processes at base of uncus. Uncus curved ventrally and tapering abruptly to a point at distal end. Dorsal edge of harpe sharply curved ventrally at distal end to form a large ventral process and from inner edge of dorsal edge of harpe a smaller terminal process. From near the base of the harpe on the ventral edge a long slender process. Scoup (juxta?) curved dorsally at end and terminating in a thorn-like spine preceded by a pair of double-pointed thorns. Aedeagus terminating in two long but unequal spines.

Strand (1915: 25), on the basis of a male and two females collected in Trinidad, named a local form *trinidadensis*. The description simply states "Without white spots on the palpal base and on the thorax. Wing expanse 41, length of forewing 20 mm. female."

Materials.—Two male specimens were collected on May 5 and June 17 at Simla.

Range.—Costa Rica to Surinam.

Calonotos craneae, new species
(Pl. I, fig. 5; Pl. II, fig. 5)

Length of forewing of males and females average 19-20 mm. Females average but slightly larger than males.

Antennae of male bipectinate with the distal end of each pectination dilated and bristled. The pectinations on each side of the antennal shaft subequal. In the female the antennae are similar, but the pectinations are shorter than in the male and the pectinations on the inside of the antennal shaft of the female are very short in comparison with the pectinations on the outer side of the antennal shaft. Antennae in both sexes with the pectinations decreasing in size towards the apex of the shaft. The dorsal side of the distal end of the antennal shaft white (approximately the distal fifteen segments) but with the terminal one or two segments brown.

Palpi normal in shape and position for the genus. The fan-shaped tuft on the base of the first segment of the palpi concolorous brown, as well as the three palpal segments.

Front of head blackish-brown with two white spots on upper lateral edges below antennae. Vertex of head, collar, tegulae, thorax and legs concolorous dark brown. A small amount of white on the distal end of the hindcoxae in both sexes but smaller and less conspicuous in the female. In some lights there is a slight bluish-green reflection from the dark brown of the various structures mentioned above.

Forewings blackish-brown. Typically with three white spots, one elongate spot below the middle of the discal cell, a subspherical spot beyond the cell bordering on the discoidal veins proximally and between vein M_1 and vein M_2 and a third spot between veins Cu_1 and Cu_2 . However, this last-mentioned spot is always smaller in the males than in the females and may be absent, although usually a few white scales persist. In addition, in one female this same spot is so enlarged as to extend half way between veins Cu_2 and M_3 . A short iridescent blue sub-basal streak on upper edge of basal third of cell but not extending to base of wing. In two males and one female there is a short iridescent blue streak within the basal part of the discal cell.

Hindwing concolorous black-brown with one white hyaline spot beyond the cell.

Underside of forewing concolorous dark brown except for the inner margin below the anal vein which is light brown. The underside of the hindwing concolorous dark brown with iridescent blue-green patches above and within the discal cell. The whitish-hyaline spots on the upper side of the wings are present on the underside of the wings.

Abdomen shining iridescent, silvery blue with two longitudinal subdorsal black-in-brown stripes. The basal segment black-brown with two gray or whitish subdorsal spots. These spots are seldom conspicuous and may be all but absent. Two lateral white spots on bullae which are larger than the subdorsal spots. A narrow blackish-brown lateral stripe with a very narrow stripe below of iridescent silvery blue ground color. This silvery blue stripe diminishes and finally disappears on the terminal segments of the abdomen. The ventral surface of the abdomen blackish-brown with a midventral white stripe. This white stripe is always present but is stronger in some specimens than others.

Male genitalia massive and symmetrical. A pair of appendages arises cephalad and dorsad of the uncus. These processes extend caudally beyond the uncus and have a lobe-like structure subventrally at their bases. The base of the uncus is in the plane of the tegumen, but the uncus narrows and bends ventrally at right angles for a distance longer than its horizontal length. The harpe with two processes. One process long and slender with long hair on its ventral edge produced from the ventral edge of the harpe. The ventral edge of the harpe narrows abruptly after this process to produce just before the terminus of the harpe a small slender process directed ventrally. Scoup (juxta ?) long, broad and massive, terminating in two long processes bent at right angles in a dorsal direction.

Most closely related to *triplagus* Hampson and *chalcipleurus* Hampson. In both of these species, as in *craneae*, the iridescent blue mid-dorsal line commences at the anterior edge of the second abdominal segment rather than at the anterior edge of the first abdominal segment which is characteristic of *tripunctatus*. The wing expanse of the holotype of *triplagus* is 38 mm. as against 42-45 mm. of *craneae*. The collar of *triplagus* has paired white spots while *craneae* is concolorous black-brown. The dorsum of the thorax is spotted metallic green in *triplagus* but is immaculate black-brown in *craneae*. The coxae and extremities of the femora are spotted white in *triplagus* and unspotted in *craneae*. The hyaline white on the wings of *triplagus* and *craneae* appear to be similar. The type locality of *triplagus* is Manaos, Brazil. The legs and thorax are also spotted white in *chalcipleurus* and the dorsum of the thorax with golden green spots, contrary to *craneae* in which these areas are black-brown. The pectinations of the antennae appear to be longer in *chalcipleurus* than in *craneae*. The ventrum of the abdomen with a series of white spots in *chalcipleurus*, whereas in *craneae* it has a ventral white stripe. Hampson

gives the wing expanse of *chalcipleurus* as 46 mm., which is considerably larger than *craneae*.

I take pleasure in naming this species after Jocelyn Crane, Assistant Director of the Department of Tropical Research, New York Zoological Society.

All of the type material was collected at Simla, Arima Valley, Trinidad. Holotype, male, Catalog No. 5656, I-VI; allotype, female (5657) 25-IV; paratypes, 29 males, (5658) 3-I, (5659) 7-I (5660) 11-I, (5661) 11-I, (5662) 12-III, (5663) 27-III, (5664) 2-IV, (5665) 2-IV, (5666) 3-IV, (5667) 6-IV, (5668) 8-IV, (5669) 16-IV, (5670) 18-IV, (5671) 25-IV, (5672) 25-IV, (5673) 27-IV, (5674) 29-IV, (5675) 1-V, (5676) 2-V, (5677) 4-V (5678) 7-V, (5679) 8-V, (5680) 10-V, (5681) 12-V, (5682) 12-V, (5683) 13-V, (5684) 13-V, (5685) 28-V, (5686) 1-VI; 23 females, (5687) 7-I (5688) 5-II, (5689) 13-II, (5690) 20-II, (5691) 27-II, (5692) 28-II, (5693) 2-III, (5694) 6-III, (5695) 7-III, (5696) 14-III, (5697) 20-III, (5698) 27-III, (5699) 27-III, (56100) 29-III, (56101) 4-IV, (56102) 19-IV, (56103) 27-IV, (56104) 3-V, (56105) 4-V, (56106) 6-V, (56107) 16-V, (56108) 28-V, (56109) 1-VI.

Disposition of type material.—The Department of Tropical Research, New York Zoological Society, will retain four paratypes, Catalog Nos. 5662, 5669, 5699 and 56108. Paratypes with Catalog Nos. 5683 and 56106 are in the British Museum (Natural History) collections and paratypes with Catalog Nos. 5682 and 56109 are in the United States National Museum collections. The holotype, allotype and remaining paratypes are in the American Museum of Natural History, New York.

Calonotus tripunctatus Druce
(Pl. III, fig. 33)

Calonotus tripunctatus Druce, 1898: 401.

Calonotus tripunctatus, Hampson, 1898: 335 (in part), pl. XII, fig. 7.

Calonotus tripunctatus, Draudt in Seitz, 1915: 109, fig. 18a.

Calonotus tripunctatus, Kaye & Lamont, 1927: 7.

Superficially similar to *craneae* but may be easily separated by the dorsal green band in *tripunctatus* running to the thorax and no white points on either side of this line on the basal segment of the abdomen.

Kaye & Lamont synonymized *chalcipleurus* Hampson under *tripunctatus*, and while I have not seen *chalcipleurus*, it appears to be a valid species. First of all the basal abdominal segment of *chalcipleurus* is black-brown as in *craneae* and *tiburtus* and does not have the dorsal silvery blue that is present on *tripunctatus*. A pair of subdorsal white spots above the bullae on the basal abdominal segment of *chalcipleurus* which is absent in *tripunctatus*. The thorax and legs of *tripunctatus* are black-brown, whereas in *chalcipleurus* the legs and thorax are spotted white with the dorsum of the thorax with metallic green spots. The type locality of *chalcipleurus* is Aroa, Venezuela.

Male genitalia with large flat lobes on base of uncus. Uncus curved ventrally with distal end inflated but with acuminate terminus. Harpe with ventral process long and slender and dorsal process with a broad ventral spine near bifurcation of dorsal and ventral harpal processes and a long finger-like process directed caudally at approximately the mid-point. Terminus of the dorsal process blunt. Scoup (juxta ?) with a single small spine at caudal end and directed laterally. Caudal end of aedeagus with long process at one side.

One female collected on May 14 with a Catalog Number 5491 is provisionally placed in this species. It has only one white spot on the forewing but otherwise appears identical.

Material.—Twenty-one specimens (7 males and 14 females).

Range.—Holotype from Trinidad. Reported from St. Vincent and Venezuela.

EXPLANATION OF THE PLATES

PLATE I

- FIG. 1. *Pseudosphex kenedyae*, dorsolateral view of male genitalia.
 FIG. 2. *Pheia beebei*, lateral view of male genitalia.
 FIG. 3. *Saurita arimensis*, dorsal view of male genitalia.
 FIG. 4. *Macrocneme spinivalva*, dorsal view of male genitalia.
 FIG. 5. *Calonotos craneae*, lateral view of male genitalia.

PLATE II

- FIG. 1. *Pseudosphex kenedyae*, new species. Holotype.
 FIG. 2. *Pheia beebei*, new species. Holotype.
 FIG. 3. *Saurita arimensis*, new species. Holotype.
 FIG. 4. *Macrocneme spinivalva*, new species. Holotype.
 FIG. 5. *Calonotos craneae*, new species. Holotype.

PLATE III

The following figures are of species collected at Simla, Arima Valley, Trinidad, except for *Cosmosoma achemon* collected at St. Augustine, Trinidad.

- FIG. 1. *Pleurosoma trinitatis* ♀.
 FIG. 2. *Sphecops aurantiipes* ♂.
 FIG. 3. *Phoenicoprocta vacillans (nigropeltata)* ♂.
 FIG. 4. *Phoenicoprocta vacillans* ♀.
 FIG. 5. *Phoenicoprocta vacillans* ♀.
 FIG. 6. *Loxophlebia bisigna* ♂.
 FIG. 7. *Loxophlebia postflavia* ♂.
 FIG. 8. *Mesothen endoleuca* ♂.
 FIG. 9. *Mesothen pyrrha* ♂.
 FIG. 10. *Chrostosoma viridipunctatum* ♂.
 FIG. 11. *Cosmosoma rubriscapulae* ♀.
 FIG. 12. *Cosmosoma subflamma subflamma* ♂.
 FIG. 13. *Cosmosoma melathoracia* ♂.
 FIG. 14. *Cosmosoma anoxanthia* ♂.
 FIG. 15. *Cosmosoma achemon* ♂.
 FIG. 16. *Cosmosoma klagesi* ♂.
 FIG. 17. *Dixophlebia holophaea* ♂.
 FIG. 18. *Pseudomya melanthus* ♂.
 FIG. 19. *Pseudomya melanthus* ♀.
 FIG. 20. *Rhynchopyga flavicollis* ♂.
 FIG. 21. *Saurita cassandra* ♂.
 FIG. 22. *Saurita clusia* ♂.
 FIG. 23. *Saurita clusia* ♀.
 FIG. 24. *Saurita afflicta* ♂.
 FIG. 25. *Saurita afflicta* ♀.
 FIG. 26. *Dycladia basimacula* ♂.
 FIG. 27. *Histiaea meldolae* ♂.
 FIG. 28. *Histiaea cepheus* ♂.
 FIG. 29. *Macrocneme plumbea* ♂.
 FIG. 30. *Macrocneme vittata* ♂.
 FIG. 31. *Macrocneme thyra intacta* ♂.
 FIG. 32. *Calonotos tiburtus* ♀.
 FIG. 33. *Calonotos tripunctatus* ♂.



FIG. 1



FIG. 2



FIG. 3



FIG. 4



FIG. 5

THE CTENUCHIDAE (MOTHS) OF TRINIDAD, B.W.I.
PART I. EUCHROMIINAE



FIG. 1



FIG. 2



FIG. 3



FIG. 4



FIG. 5

THE CTENUCHIDAE (MOTHS) OF TRINIDAD, B.W.I.
PART I. EUCHROMIINAE



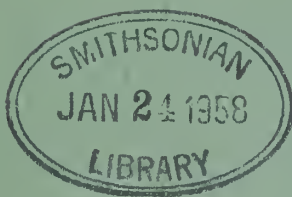
THE CTENUCHIDAE (MOTHS) OF TRINIDAD, B.W.I.
PART I. EUCHROMIINAE

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The Ability of the Saprolegniaceae to Parasitize Platyfish¹

HELEN S. VISHNIAC & R. F. NIGRELLI

Department of Microbiology, Yale University, and
New York Aquarium, N. Y. Zoological Society

(Plate I)

A NUMBER of species of fungi belonging to the Saprolegniaceae have been isolated from naturally occurring infections in fish and other aquatic animals (Table 1). The list is so diverse, from a taxonomic point of view, as to suggest that any saprolegniaceous fungus might be capable of parasitism under appropriate conditions. The experiments reported here were undertaken to determine whether genera and species not previously reported to be parasitic, as well as saprophytic isolates of species known as parasites, could infect platyfish under conditions which allowed infection by two fungi isolated from naturally occurring infections. The platyfish is known to be susceptible to *Saprolegnia* (Gordon, 1936). However, there is no evidence of host specificity for these fungi even though there is variation in the susceptibility of different fish in captivity (Tiffney, 1939a) as well as in nature. Tiffney (1939a) reported that *Saprolegnia parasitica* can attack at least 16 species of fishes and 2 species of amphibians. *Saprolegnia parasitica* also attacks aquatic reptiles both in nature and in captivity. Other species have been reported in crustaceans (Atkins, 1954; Höhnk & Vallin, 1953; Prowse, 1954; Smith, 1940), lamellibranchs (Atkins, 1954),

larval mosquitoes (Rioux & Achard, 1956) and rotifers (Valkanov, 1931).

Mycosis caused by Saprolegniaceae is a disease of temperate and tropical freshwater and possibly brackish water fishes. Those affecting temperate water fishes, e.g. carp, have been recognized in Central Europe since the Middle Ages. The number of fish species susceptible to infections by Saprolegniaceae has never been properly recorded. From more than 25 years' experience with the diseases of fish, it can be stated without exaggeration that most freshwater fishes are susceptible to infection by some species of Saprolegniaceae, especially under tank and hatchery conditions and following injury of the skin or gills. In fishes, primary infections occur in individuals that have lesions caused by injury. Lesions caused by protozoan and metazoan parasites are the loci of secondary infections. At the New York Aquarium, more than 45 deaths were reported in a single year as being caused by "*Saprolegnia*" (Nigrelli, 1943). A re-check of the Aquarium's records for 1939, 1940 and 1941 showed that 24 species of temperate and tropical freshwater fishes, 4 species of urodeles and 4 species of turtles died from such infections. *Saprolegnia*-like infections were also found in the feet of alligators which had developed ulcers from other causes. No efforts were made at the time to determine which species of Saprolegniaceae were involved in these deaths.

The results of our experiments indicate that although the family Saprolegniaceae is primarily saprophytic in nature, the potentiality of parasitic existence is a familial characteristic. Moreover, under our conditions, at least, the infecting fungus can be a primary invader.

¹ It is a pleasure to acknowledge our debt to Dr. Myron Gordon and the Genetics Laboratory of the New York Zoological Society for the fish used in these experiments. We are indebted to Dr. J. R. Raper, Dr. A. W. Ziegler and Dr. L. Shanor for the isolates designated by their initials. The experimental infections were made at Haskins Laboratories, New York City, in the laboratory of Dr. S. H. Hutner, for whose interest we are grateful. This study was supported in part by research grant E 1179 from the National Institute of Allergy and Infectious Diseases of the National Institutes of Health, U. S. Public Health Service.

TABLE 1. SAPROLEGNIACEAE OCCURRING AS PARASITES OF AQUATIC ANIMALS

Fungus	Reference
<i>Achlya flagellata</i>	see Tiffney, 1939b
<i>A. polyandra</i>	see Tiffney, 1939b
<i>A. prolifera</i>	see Tiffney, 1939a, b
<i>A. racemosa</i>	see Tiffney, 1939b
<i>Achlya</i> sp.	Tiffney, 1939b
<i>Aphanomyces laevis</i>	Smith, 1940
<i>Ap. astaci</i> ¹	see Prowse, 1954
<i>Ap. daphniae</i> ¹	Prowse, 1954
<i>Ap. hydatinae</i> ¹	Valkanov, 1931
<i>Ap. ovidestruens</i> ¹	see Prowse, 1954
<i>Dictyuchus monosporus</i>	Tiffney, 1939b
<i>Leptolegnia baltica</i>	Höhnk & Vallin, 1953
<i>L. caudata</i>	see Coker, 1923
<i>L. marina</i>	Atkins, 1954
<i>Saprolegnia diclina</i>	Rioux & Achard, 1956
<i>S. ferax</i>	see Tiffney, 1939a, b
<i>S. mixta</i>	see Tiffney, 1939b
<i>S. monoica</i>	see Tiffney, 1939a, b
<i>S. parasitica</i>	see Tiffney, 1939a, b
<i>S. torulosa</i>	see Tiffney, 1939b

¹ If these are indeed valid species.

MATERIALS AND METHODS

The 19 isolates of saprolegniaceous fungi used are listed in Table 2. *Brevilegnia unisperma* and *Dictyuchus monosporus* were originally included in this group, but were omitted when they failed to produce zoospores under the conditions of the experiments, since infection in nature is normally accomplished by zoospores (Tiffney, 1939a). Two of the fungi listed were isolated from naturally infected aquarium fish: *Achlya* sp. from an electric catfish (*Malapterurus electricus*) and *Saprolegnia parasitica* from the mosquito fish (*Gambusia affinis*).

The *Achlya* sp. was similar to the sterile *Achlya* described by Tiffney (1939b) from the shell of *Chelydra serpentina*, except in the appearance of the "chlamydospores." In our isolate, these structures were spherical to ovoid, never clavate. They were formed first terminally, later on racemose branches or less frequently in basipetal chains. These "chlamydospores" were shown in our isolate to be oogonia. When mats (grown in pure culture) of *Achlya* sp. were placed in a petri dish in proximity to mats of male (E247) and female (355) thalli of *A. bisexualis*, abundant antheridial initials formed on E247 within three to four hours. After 24 hours, well differentiated oospheres could be seen in the "chlamydospores" of *Achlya* sp. A few eccentric oospores maturing in the oogonia of *Achlya* sp. attested to the completion of the mating reaction with E247. There was no reaction between our *Achlya* sp. and the female isolate 355. This fungus cannot, however, be considered a female

isolate of *A. bisexualis* or of any other described heterothallic species of *Achlya*. Not only were the majority of oospores aborted in the mating just described, but the characteristic of producing oogonial initials in the absence of hormonal stimuli provided by the presence of antheridial initials is present in no other heterothallic *Achlya* (see Raper, 1955). Since specific distinctions in this family of fungi are made largely on the basis of characteristics of sexual reproduction, we consider it inadvisable to formally describe this species in the absence of a male isolate giving a normal complete mating reaction.

TABLE 2. THE ABILITY OF VARIOUS SAPROLEGNIACEAE TO INFECT PLATYFISH

Fungus Present	Uninfected Fish		Infected Fish	
	Alive	Died	Alive	Died
None	2	2	0	0
None	4	0	0	0
<i>Achlya</i> sp.	1	0	1	2
<i>A. ambisexualis</i> E87 ♂ (J.R.R.)	0	0	0	4
<i>A. ambisexualis</i> 302 ♀ (J.R.R.)	0	0	0	4
<i>A. bisexualis</i> E247 ♂ (J.R.R.)	0	0	0	4
<i>A. bisexualis</i> 355 ♀ (J.R.R.)	0	0	0	4
<i>A. glomerata</i> (A.W.Z.)	2	2	0	0
<i>A. Klebsiana</i> (L.S.)	0	0	0	4
<i>A. Sparrowii</i> ¹	0	0	0	4
<i>Aphanomyces</i> <i>laevis</i> (A.W.Z.)	0	0	0	4
<i>Calyptrolegnia</i> <i>achlyoides</i> (L.S.)	0	0	2	2
<i>Isoachlya</i> <i>monilifera</i>	3	0	0	1
<i>Protoachlya</i> <i>paradoxa</i> (L.S.)	0	1	0	3
<i>Saprolegnia</i> <i>delica</i> (L.S.)	0	0	0	4
<i>S. ferax</i>	0	0	0	4
<i>S. megasperma</i> ²	0	1	0	3
<i>S. mixta</i>	0	0	0	4
<i>S. parasitica</i>	1	0	0	3
<i>Thraustotheca</i> <i>clavata</i>	0	0	0	4
<i>T. primoachlya</i> ² (A.W.Z.)	0	0	2	2

¹ Johnson (1956) considers this species to be synonymous with *A. racemosa* Hildebrand. Since *A. racemosa* has centric oospores while *A. Sparrowii* has subcentric oospores (a distinction which Johnson considers, in the same study, to be of subgeneric rank), we prefer to retain *A. Sparrowii*.

² Two broods of young were born in the course of this experiment. Normal young (9 and 5) remained healthy; premature fry (i.e. with visible yolk sac) became parasitized and died (5 and 3). It was the mother of one of these broods that died without becoming parasitized by *Saprolegnia megasperma*.

The Mexican platyfish, *Xiphophorus maculatus*, was used as host in these experiments.

The conditions chosen for these experiments were determined, by means of preliminary experiments, to provide the greatest chance of infection by the two parasitic isolates (*Achlya* sp. and *Saprolegnia parasitica*) together with the lowest mortality from causes other than induced fungal infection. Pyrex kitchen trays (ca. 8"×12"×2") were washed thoroughly, steamed, filled with 1.5 liters of tap water, and placed on an illuminated bench at room temperature (approximately 20° during the course of these experiments). An excess of fish food was then placed in them and inoculated with a pure culture of a fungus. When the growth of the fungus on the fish food was producing an abundance of zoospores, four platyfish, roughly evenly distributed as to size and sex, were placed in each tray, together with a few strands of *Nitella*. Just before exposure to the fungi, these fish were injured by scraping the scales from an area approximately 2×2 mm. on one side of the caudal peduncle. Uninjured fish were not attacked; fish injured by mere rubbing or nicking of the caudal peduncle were not consistently attacked. The fish were then observed until death, at which time they were removed from the tray, examined to verify the identity of the fungus and preserved in formalin (Plate I), or until the disappearance of the fungus from the tray.

Paraffin sections of the diseased peduncle were prepared and stained with haematoxylin-eosin and with Masson's trichrome stain; whole mounts of the skin and scales showing the mycelia were treated with a modification of Malory's method in which the following stains were used: Harris' haematoxylin, Phloxin B and Stirling's anilin crystal violet. The tissues were then treated with Gram's iodine and differentiated with several changes of anilin oil until no more color was removed. The stained material was then passed through several changes of xylene and mounted in Permout. With this method, the mycelia stained blue and the sporangia red and the extent of the infection was followed with ease.

RESULTS

The results of these experiments are given in Table 2. It is evident that under the conditions which permit infection by the two parasitic isolates, nearly every saprolegniaceous fungus used can attack, and usually kill, platyfish. The two apparent exceptions, *Achlya glomerata* and *Isoachlya monilifera*, did not in fact present quite the same conditions as the parasitic isolates. *Achlya glomerata* grew sparsely, although what

growth there was produced zoospores. *Isoachlya monilifera* grew moderately well before the addition of the fish, which promptly ate up the mycelium, thus greatly reducing their chance of infection. Consumption of mats of living mycelium of *Saprolegnia parasitica* by fish which suffered no harm thereby has been noted by Tiffney (1939a). The fungus appearing on infected fish was in every case the species with which the tray had been inoculated.

The first signs of infection always appeared at the injured area on the caudal peduncle in the form of a tuft of hyphae. Later, in fatal infections, hyphae often emerged from the gills and mouth, and in tufts over the body, or the entire fish became covered with the fuzzy growth of the fungus.

The pathological lesions were more or less similar, varying only in degree. In relatively light infections, the mycelia penetrated the epithelium of the scales and skin with some necrosis of the involved areas. In heavy infections, the epithelium was often sloughed and the scales and fin rays were softened or completely destroyed. The growth penetrated the deeper tissues, the hyphae often passing into the muscle bundles and resulting in hyalinization or complete destruction. Macrophages filled with melanin, cellular debris and blood cells, together with lymphocytes, were invariably found massed in the areas of the mycelial growth. Inflammatory reaction of varying intensity occurred in regions immediately adjacent to the infection. Surprising as it may seem, little or no bacterial infection was present in any of the sections studied, indicating that the tissue destruction was due almost exclusively to the fungi.

DISCUSSION AND CONCLUSIONS

The criteria listed by Henle in 1840 for establishing a causal relationship between an organism and a disease in its putative host begin with the isolation of the organism from cases of the disease. We have shown that given a set of conditions which allow infection by two saprolegniaceous fungi isolated from diseased fish, all other saprolegniaceous fungi for which the same conditions (including abundant sporulation) could be provided would infect platyfish. Some of the species used, although not isolated from diseased animals in this instance, have previously been reported to be parasitic, viz. *Aphanomyces laevis*, *Saprolegnia ferax* and *S. mixta*. The remaining 12 species have not been so reported. Since from these results and previous reports at least 27 species in 10 genera of the Saprolegniaceae have been found capable of attacking animal hosts, we may conclude that

potential parasitism is a familial characteristic. But from the ecological point of view the 12 species not known to be involved in natural infections are not parasites. There is, to be sure, a very marked difference in frequency of occurrence of reported parasites. *Saprolegnia parasitica* is universally reported as most common; other species are reported in frequencies ranging down to only a single established case. It would hardly be surprising if continued search should disclose that the forms we have designated as potential parasites are actually parasitic in nature. The reasons for the rarity or absence of the parasitic habit in some species of this family are probably to be found in their specific ecology. A successful parasite in nature must be abundantly sporulating under the conditions of temperature, etc., that exist when and where susceptible animals appear. While the report of Coker (1923) on seasonal occurrence of saprolegniaceous fungi and the extensive studies of Höhnk (1934, 1956), of Höhnk & Bock (1955) and of Bock (1956) are outstanding as contributions to our knowledge of the specific ecology of the Saprolegniaceae, more precise quantitative techniques would be desirable before attempts are made to correlate the production of zoospores and infections by various species of the Saprolegniaceae in nature.

SUMMARY

Eighteen of 19 isolates of saprolegniaceous fungi, including 16 species belonging to 7 genera, infected platyfish having a standardized wound on the caudal peduncle. The infection usually resulted in the death of the fish. Histological examination indicated that tissue destruction was due almost exclusively to the infecting fungus.

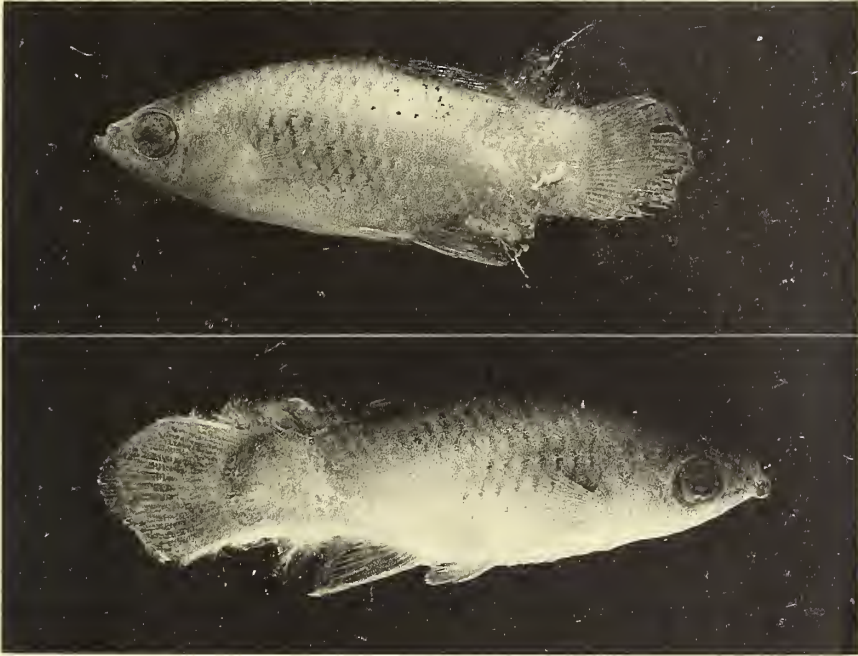
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EXPLANATION OF THE PLATE

PLATE I

- FIG. 1. Platyfish infected with *Isoachyla monilifera* (upper) and *Saprolegnia megasperma* (lower). Preserved in formalin. 2X.



THE ABILITY OF THE SAPROLEGNIACEAE TO PARASITIZE PLATYFISH

Imaginal Behavior in Butterflies of the Family Heliconiidae: Changing Social Patterns and Irrelevant Actions¹

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(Plate I)

[This paper is one of a series emanating from the tropical Field Station of the New York Zoological Society at Simla, Arima Valley, Trinidad, British West Indies. The Station was founded in 1950 by the Zoological Society's Department of Tropical Research, under the direction of Dr. William Beebe. It comprises 200 acres in the middle of the Northern Range, which includes large stretches of undisturbed government forest reserves. The laboratory of the Station is intended for research in tropical ecology and in animal behavior. The altitude of the research area is 500 to 1,800 feet, with an annual rainfall of more than 100 inches.

[For further ecological details of meteorology and biotic zones see "Introduction to the Ecology of the Arima Valley, Trinidad, B.W.I.," William Beebe. (Zoologica, 1952, Vol. 37, No. 13, pp. 157-184.)]

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I. INTRODUCTION

THIS contribution is one of a series on the biology and ecology of butterflies of the neotropical family Heliconiidae. It concerns post-imaginal changes in social behavior patterns, and various kinds of irrelevant behavior, including the displacement of actions

characteristic of one pattern by actions from another behavioral field.

The observations presented arose as unexpected incidental results of a comparative ethological study of six species common on the island of Trinidad, British West Indies. The publication of these data appears to be a prerequisite to the adequate exposition of comparative specific characteristics and to an illumination of the group's phylogeny. A first paper in the series, on *Heliconius erato hydara* Hewitson, has been published in which the effect of age on behavior and the occurrence of displacement behavior were mentioned (Crane, 1955). Five additional species, along with *H. erato*, are considered below. These consist of *Dryas julia julia* (Fabricius), *Heliconius melpomene euryades* Riffarth, *H. sara rhea* Cramer, *H. ricini insulana* Stichel and *H. isabella isabella* Cramer. Details of their behavior patterns, accounts of releasing mechanisms and discussion of phylogenetic aspects are being reserved for more appropriate inclusion in forthcoming contributions.

The risks of inaccuracy and incompleteness in the description of butterfly behavior became apparent very early in the work, particularly in the study of courtships. The patterns seemed at once surprisingly variable within a species, unexpectedly similar among species and altogether too unpredictable to be characteristic of arthropods, with their high degree of dependence on stereotypic forms of behavior.

Since the butterflies were being studied principally in outdoor insectaries, it was thought at first that the discrepancies might be the result of unnatural conditions—although even if that were so the interest of the variability of the behavior would scarcely have been lessened.

¹Contribution No. 979, Department of Tropical Research, New York Zoological Society.

Enough corroborative observations have now been made in the field, however, to show that the apparent eccentricities are equally characteristic of free-flying butterflies. Further corroboration of the natural prevalence of the types of behavior under consideration comes from the fact that, now that the causes are better understood, the patterns shown in the insectaries are highly predictable.

Some of the behavioral discrepancies have proved to be due simply to age differences in the individuals observed. The full courtship pattern characteristic of the species, for example, is elicited only in and by individuals between certain ages, although successful reproduction can take place throughout a much longer portion of imaginal life.

Other irregularities appear when, as Tinbergen (1952, p. 26) defines the conditions for displacement activities, "a strongly activated drive is denied discharge through its own consummatory act(s)." However, in the present paper the term "irrelevant behavior" (suggested by Rand, 1943) will be employed as a more general term than "displacement behavior." The latter, it seems, may be usefully restricted to the definition given by Bastock, Morris & Moynihan (1953, p. 25): "A displacement activity is an activity belonging to the executive motor pattern of an instinct other than the instincts activated."

This distinction between terms seems desirable since some of the butterfly actions under consideration do not at all appear to belong to the motor pattern of another instinct, and hence will be simply referred to as "irrelevant actions." Others, which fulfil the conditions of the more restricted definition of displacement activities, will be so designated here and treated as a subdivision of irrelevant actions.

My thanks go to the National Geographic Society for a grant-in-aid, to Dr. William Beebe, Mr. Henry Fleming and Dr. D. W. Snow for helpful suggestions, and to Miss Barbara P. Young for rearing numerous larvae.

II. HISTORICAL REVIEW

The special aspects of social behavior under consideration are little-known fields in the study of invertebrates.

The gradual development of behavior patterns in physiologically adult vertebrates has been extensively studied, and it is well known that changes occur in response to physiological alterations due both to increasing age and to seasonal causes.

Corresponding information has been gathered on few invertebrates, although the Hymenoptera include outstanding exceptions. The

sequence of changes in colony functions have been studied in worker honeybees (Rösch, 1925), *Polistes* (Steiner, 1932) and in various ants (e.g. Buckingham, 1910). Verlaine (1932) reported differences between young and old mason wasps in nest-repairing and provision behavior, that of old bees late in the season being incomplete; this observation invalidated a conclusion drawn by Fabre (1879; ed. 1920) from experiments which he performed, using aged individuals. Pardi (1947) found that age was one of the factors determining the status of individual *Polistes* females in a dominance hierarchy. Nielsen & Nielsen (1952) reported that the migratory period of a pierid butterfly (*Astia*) was confined to a single day of the five-day life-span. As an example of intrageneric variation, the parasitic wasp genus (*Opius*) may be cited: males of certain species cannot mate for five days or more after emergence, although in other species they do so early in the imaginal period (Hagen, 1953). Finally, entomologists would probably agree that female insects that have recently molted into the final instar are in general more attractive to males than are older individuals. It will be noted, however, that use of the inexact term "recently" is necessary.

Rockstein (1956) discussed the unreality of a sharp boundary between the pupal and imaginal stages in insects, citing recent research on biochemical changes occurring after emergence in the worker honeybee, house fly, *Drosophila*, moths and the Japanese beetle. In *Drosophila* there are concomitant increases in glycogen content and wing-beat frequency during the first week of imaginal life. Although this frequency change is not directly related to social behavior, the phenomenon illustrates the kind of correlation which may be brought to light in investigations linking invertebrate physiology and behavior.

Studies of irrelevant actions, including displacement behavior, in vertebrates are increasing in number, following the pioneer work of Lorenz, Tinbergen, Makkink, Koorlandt and Armstrong. General accounts and references are given by Armstrong (1950), Lorenz (1950), Tinbergen (1951, 1952), and Bastock, Morris & Moynihan (1953). Recent studies on particular species of birds and fish include those of Hinde (1953), van Iersel (1953), Moynihan (1953) and Morris (1954).

The probable occurrence of equivalent behavior in invertebrates has apparently not been suggested until recently. Armstrong (1950, pp. 379 ff.) summarized the situation as it appeared at the time of his writing as follows: "Probably displacement activities are commoner in some other groups besides birds than is at present

known, but they have reached their highest development in birds . . . So far as is at present known they have a comparatively insignificant role among insects. A thwarted solitary wasp, *Bembex rostrata*, when forced to remove pebbles repeatedly from the mouth of its burrow merely buzzed loudly and ran around in a wide arc (Nielsen, 1945). When experimenting with butterflies attracted to pieces of coloured paper Dr. D. Ilse noticed movements which might have been displacement activities (personal communication). Possibly one of the factors responsible for the apparently slower speciation of insects than birds (Mayr, 1942) is the greater displacement-proneness of the latter."

A few recent observations and comments, however, suggest that displacement activities may prove, after all, to be widespread among higher arthropods. References to date appear to be confined to the following: salticid spiders (Crane, 1949), mantids (*idem*, 1952), the butterfly *Heliconius erato* (*idem*, 1955), *Drosophila* (Bastock & Manning, 1955) and fiddler crabs, genus *Uca* (Gordon, 1955, and Crane, 1957).

III. MATERIAL AND METHODS

The studies were all conducted in out-of-door wire mesh insectaries in Trinidad (Crane & Fleming, 1953; Crane, 1955) between 1954 and 1957. During the past two seasons a new insectary, designed as were the earlier ones by Henry Fleming, has been in operation. Constructed entirely of aluminum, it measures 24 × 36 feet, the dimensions of the larger of the two earlier structures, but it is higher than its predecessor, measuring 12 feet at the ridgepole. It also has two doors with a small vestibule between, forming a baffle which has proved very useful in preventing the escape of butterflies. A small pond and bog have been added near one end; they form an efficient aid in maintaining the necessary high humidity.

The aluminum netting reflects far more heat than does bronze mesh; it also diffuses the light better, making it excellent for photography. Finally, species suitable for keeping in a cage of this size tend to bat against the netting less, even when they have just been released into it, than they did against the bronze netting of the previous insectary.

For this reason, as well as because of the insectary's relative coolness, heavy vines giving large areas of dense shade have been found to be not only unnecessary but undesirable. Instead, the planting is kept to several well-separated major groups of shrubs, saplings and wild bananas of varying degrees of height, density and leaf size. The rest of the space is occupied

by flowering weeds and by the pond. Branches with bromeliads attached stand upright at intervals against the netting, as a further aid in maintaining humidity and natural conditions. The wild banana group (*Heliconia*) beside the bog forms the coolest, most shady corner of the cage. *H. erato*, *melpomene* and other shade-lovers invariably seek it out during the heat of the day. In contrast, other species, such as *H. isabella*, which is most active around noon, frequent the open center of the cage around a group of *Lantana*, *Bidens* and *Asclepias*. In this cage all of the latter, favorite food blossoms of the heliconiids, thrive and are allowed to grow freely over most of the cage. This scattering of a natural food supply encourages a normal amount of flight by the butterflies.

The success of the new design is attested by the fact that all of the six species (p. 135) of heliconiids discussed in the present paper feed, court, mate and lay eggs. Many individuals remain alive, barring accidents, for one to three and one-half months, although differences in viability are shown. *H. isabella* is the most difficult to maintain, and observations on this species are still somewhat deficient. Two locally rare heliconiids, *Philaetrea dido* (Linnaeus) and *Heliconius wallacei* Reakirt, have not been successfully maintained. They live a few days and feed, but do not "settle in" and spend most of their active periods batting against the roof. Presumably a higher cage is needed.

Broods from all the species of heliconiids included in this study were raised in the laboratory. The young imagoes were kept in small cages out-of-doors until needed for observation or testing in the large insectary. General methods are given in an earlier paper (Crane, 1955).

Table 1 gives an idea of the number of healthy imagoes that were used in the preparation of this study. Substandard specimens, as well as those observed in the early seasons before techniques were perfected and the present problems formulated, are not included.

IV. SURVEY OF SOCIAL BEHAVIOR IN SIX SPECIES OF TRINIDAD HELICONIIDAE

The social behavior of all six of the Trinidad species discussed below consists of three general types—courtship, "social chasing" and roosting. These have already been described in some detail for *H. erato* (Crane, 1955). Except for minor differences they are characteristics of the other five species as well. Although these slight specific differences are of great potential interest from a phylogenetic point of view, their detailed discussion belongs in subsequent papers on the ethology of the genus.

TABLE I. NUMBERS OF INDIVIDUALS UPON WHICH PRESENT DATA ARE BASED

(From broods reared during the seasons of 1954-1957, incl.).

Species	Males	Females
<i>Dryas julia</i>	49	46
<i>Heliconius melpomene</i>	27	28
<i>Heliconius erato</i>	71	62
<i>Heliconius ricini</i>	38	27
<i>Heliconius isabella</i>	21	22
<i>Heliconius sara</i> (1957 only)	16	19

A. COURTSHIP. Since the similarities of the behavior within the genus are far greater than the differences, a comparative chart (Table 2) of the patterns of fully developed courtship will indicate the trends to the extent needed for present purposes.

It will be seen from the table that courtship usually begins and always ends similarly in all species, while differentiation is shown principally in the first and second stages of the second, sedentary phase.

In brief summary, the sequence in its most complete form is as follows:

1. Aerial Phase.

Stage I. Nudging. A flying male approaches a resting female from the rear. She then takes wing, usually without his actually touching her in any way.

Stage II. Flight. The male chases and overtakes the female, rises above and in front of her and fans her with the rapid vibration of his wings, so spreading the products of his scent scales. She then descends or is forced down to a perch. Chases sometimes include mutual circling and spiralling in all the species. At these times the circling by the female is apparently always merely the result of her temporarily successful effort to duck out from under and behind the flying male and rise above and in front of him; he in turn repeats the manoeuvre and the resulting vertical circling may continue for several minutes. Horizontal spiralling is less frequent but seems to have a similar basis. In the previously published account of *erato* (Crane, 1955) this flight stage, which is little developed in that species and often omitted, was not separated from Stage I of the Sedentary Phase below.

2. Sedentary Phase.

Stage I. Primary Fanning. The male fans the alighted female from the front or rear, de-

pending on the species, facing in the same direction as the female. The latter, meanwhile, flutters her wings, also characteristically, elevates the abdomen and, in this stage or the next, extrudes the subterminal scent glands.

Stage II. Secondary Fanning. The male fans the female from a different position from that in Stage I, but still facing in the same direction as she. The female meanwhile extrudes the subterminal scent glands if she has not already done so.

Stage III. Alighting and Engaging. The male alights beside the female, either just in front of or just behind her, moves back or forward appropriately and, as she closes her wings, curves his abdomen up between her posterior wings, engages her genitalia with his harpes, and swings around so that the two insects now face in opposite directions.

B. SOCIAL CHASING. Discussed first in 1955, by Crane, in *erato*, "social chasing" was the term given to social flights that are not apparently directly of a sexual nature. It was found to take similar form in the other five species. In all, it consists of the pursuit of males and old females by males of any age, and of either sex by old females. It will be discussed on pp. 141 and 142.

C. ROOSTING. Four of the six species roost gregariously, namely *H. erato*, *melpomene*, *ricini* and *sara*. All return to the same bush or vine, and often to the same twigs or tendrils, night after night. Usually the perch selected is dry. Although the four species tend to maintain separate roosts, *erato*, *melpomene* and *ricini* often roost together, as do *ricini* and *sara*.

A trace of gregariousness is found in *Dryas*, which sometimes hangs up for the night near one or two others of its kind. *H. isabella*, however, always roosts alone. The two latter species always hang from beneath green leaves. Roosting will be further considered on p. 139.

V. CHANGES IN SOCIAL PATTERNS WITH AGE

None of the social behavior patterns summarized in the foregoing section is fully expressed when the insect emerges from the chrysalid, and it now appears that the maturation time for the various responses is similar in all six species. Table 3 shows these periods. "Age" indicates time after emergence from chrysalid.

It will be seen from the table that the full pattern of courtship—including Stage II of the Aerial Phase and the specifically characteristic wing flutters of the Sedentary Phase—is evinced by females only on their second and third days, that is, between 24 and about 56 hours after

Species	Mating Phase			
	Stage II		Stage III	
	Male	Female	Male	Female
<i>Dryas julia</i>	Nudges rear	ification of Stage I	Alights beside ♀ head, moves backward, curves abdomen forward between ♀ wings, engages harpes, swings around to face in opposite direction from ♀	Closes wings; lowers abdomen; withdraws scent glands
<i>Heliconius melpomene</i>		<i>Dryas</i>	As in <i>Dryas</i>	As in <i>Dryas</i>
<i>Heliconius erato</i>		Stage I, but lower in-	As in <i>Dryas</i>	As in <i>Dryas</i>
<i>Heliconius ricini</i>		<i>Dryas</i>	Alights beside ♀ abdomen, moves forward, then proceeds as in <i>Dryas</i> . (Rarely alights beside ♀ head as in <i>Dryas</i>).	As in <i>Dryas</i>
<i>Heliconius isabella</i>		<i>Dryas</i>	As in <i>Dryas</i>	As in <i>Dryas</i>
<i>Heliconius sara</i>		<i>Dryas</i>	As in <i>Dryas</i>	As in <i>Dryas</i>

TABLE II. BASIC MOTION SEQUENCE IN FULLY DEVELOPED UNCOMPLICATED COURTSHIPS OF TRINIDAD HELICONIDS

Species	Aerial Phase				Sedentary Phase					
	Stage I		Stage II		Stage I		Stage II		Stage III	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
<i>Dryas julia</i>	Nudges from rear	Takes flight	Pursues; aims to fly above and in front of ♀. (Scent scales probably in use).	Aims to hack out from under and rise above ♂. Eventually alights on exposed perch.	Front fanning, facing in same direction as ♀.	All wings flattened and vibrated in narrow arc, the hindwings more flattened than forewings and vibrated more rapidly; abdomen raised; scent glands extruded	Brief dorso-posterior fanning; then return to front fanning	Intensification of Stage I	Alights beside ♀ head, moves backward, curves abdomen forward between ♀ wings, engages harpes, swings around to face in opposite direction from ♀	Closes wings; lowers abdomen; withdraws scent glands
<i>Heliconius melpomene</i>	◀ Entire Aerial Phase essentially as in <i>Dryas</i> but often omitted ▶				As in <i>Dryas</i>	All wings flattened equally and slightly vibrated; otherwise as in <i>Dryas</i>	Rear fanning, then return to front fanning	As in <i>Dryas</i>	As in <i>Dryas</i>	As in <i>Dryas</i>
<i>Heliconius erato</i>	◀ Entire Aerial Phase essentially as in <i>Dryas</i> but often omitted ▶				Rear fanning	Forewings closely appressed; hindwings flattened and quivered; otherwise as in <i>Dryas</i>	Front fanning	As in Stage I, but lower intensity	As in <i>Dryas</i>	As in <i>Dryas</i>
<i>Heliconius nicini</i>	◀ Entire Aerial Phase essentially as in <i>Dryas</i> ▶				As in <i>Dryas</i>	As in <i>H. melpomene</i>	Dorso-rear and rear fanning	As in <i>Dryas</i>	Alights beside ♀ abdomen, moves forward, then proceeds as in <i>Dryas</i> . (Rarely alights beside ♀ head as in <i>Dryas</i>).	As in <i>Dryas</i>
<i>Heliconius isabella</i>	◀ Entire Aerial Phase essentially as in <i>Dryas</i> ▶				As in <i>Dryas</i>	1st day: As in <i>H. erato</i> 2nd & 3rd days: As in <i>Dryas</i>	As in <i>Dryas</i>	As in <i>Dryas</i>	As in <i>Dryas</i>	As in <i>Dryas</i>
<i>Heliconius sara</i>	◀ Entire Aerial Phase essentially as in <i>Dryas</i> ▶				As in <i>Dryas</i>	As in <i>H. melpomene</i> , but wings vibrated strongly through wider arc	As in <i>Dryas</i>	As in <i>Dryas</i>	As in <i>Dryas</i>	As in <i>Dryas</i>

TABLE III. APPROXIMATE AGES AFTER EMERGENCE AT WHICH VARIOUS TYPES OF ACTIVITY OCCUR IN SIX SPECIES OF HELICONIIDS

Activity	Age
Flutters to ground when disturbed	1 hr.
First flight when undisturbed	2 hrs.
First feeding, rarely	6 hrs.
First feeding, usually	2nd day
Earliest copulation, female	10-30 minutes
Earliest copulation, male	3rd day
Complete courtship pattern elicited, female	2nd & 3rd days
Complete courtship pattern elicited, male	3rd day— 2¾ months
Latest copulation, unmated females	6th-8th day
Latest copulation, males (2 species)	2¾ months
First eggs laid	4th-12th day
Maximum ages reached, males and females (2 species)	3½ months

emergence. In *isabella*, it is not even possible to see all the specific characteristics at one time. During the female's first day, the wing flutters of the sedentary phase are very similar to those of *erato* and the aerial phase is, as usual, normally non-existent; yet by the second day the specialized flutter is already disintegrating into the more generalized *Dryas*-type flutter (see Table 2). In all the species after their third day the wing-flutterings of the females are diminished progressively in intensity and characteristic form.

In males, copulation does not occur until the third day (48 hours after emergence) and may not take place until the fourth or fifth; these later dates are apparently always characteristic of *H. sara*. No social activity by the males whatever is shown until the second day, 24 hours after emergence, when males sometimes nudge young females from the rear. After noon of the second day slight chasing may occur, but this behavior does not usually take place until the third day.

Unlike females, males court and can mate practically throughout life. In older males, although complete and successful courtship is swiftly elicited by second-day females, relatively little attention is paid to older unmated or egg-laying individuals.

Males chase each other freely throughout life, especially in the absence of young females, except during their first two days.

In both sexes and all species, roosting according to the species habit begins on the second or third night. Even in the most gregarious species (*erato*, *melpomene* and *sara*), however, young females often hang up for the night alone, unless courting or mating has proceeded during the late afternoon. At such times the female, too, often roosts with the group.

VI. IRRELEVANT ACTIONS

A. *Males*. Under certain conditions the courtship pattern characteristic of the various species of heliconiids becomes atypical. Instead of courtship proceeding in the usual fashion to copulation or, alternatively, to the point where one partner stops responding and both go their separate ways, the male continues special behavior that never ends in copulation. On the very rare occasions when mating soon ensues between the same partners following the first stages of this irregular behavior, the male has returned to an early stage of courtship, and then followed the typical sequence.

Irrelevant actions never begin before the male has reached Stage II of the Sedentary Phase. In other words, he is in the final phase of fanning above, in front of, or behind the alighted female, his position depending on the pattern characteristic of his species (Table 2). Sometimes the male has reached Stage III, having alighted beside the female and tried unsuccessfully to attach his harpes.

One of two major types of irrelevant behavior follows, depending on whether the female flies away and evades the male or whether she stays in place.

In the first type, having lost track of the female, the male flies about at unusual speed for up to five minutes at a time, without pausing, feeding or making any apparent "searching" motions (as he may do, on other occasions, among the vegetation). This type of behavior has been artificially induced by the observer's simply picking up the female and keeping her temporarily out of sight.

The second type of irrelevant behavior follows when the female stays alighted and often appears to the observer to be making full courting responses. The first manifestation is always poor orientation in the fanning (Pl. I, Figs. 7-8). Normally in all the species the male faces in exactly the same direction as the female, although the longitudinal axes of the two insects are usually more or less oblique to each other since the male fans characteristically from down-in-front to up-in-back. In disoriented fanning the male may face in any direction, even backward

with respect to the female, and frequently changes the direction without any regular sequence.²

After disoriented fanning has continued for any period up to five minutes in length, there are a number of alternate sequels.

Most frequently the partners separate, either the male or the female flying off, and neither one thereafter evinces either excitement or special behavior.

Occasionally the female takes wing and eludes the male, whereupon the male flies about rapidly as described under the first type of irrelevant behavior.

²In the study of *H. erato* already published (Crane, 1955), Plate I, Figs. 5 and 6, are excellent examples of disoriented fanning. A third example from the same series is published as Plate I, Fig. 8, of the present contribution. At the time these photographs were made, the existence of this type of irrelevant behavior had not been recognized. It is now clear that the sequence of still photographs in the earlier plate could not be taken, with present-day still camera apparatus, to illustrate a complete, normal consummated courtship between the same two individuals, photographed in sequence. This is because these courtships always proceed too swiftly to permit recharging of the speedlamp between flash shots. Only during the prolonged repetitions of irrelevant behavior can still photographs be made of a single pair during a consecutive period of courting behavior. A motion picture camera, operated at high speed, is of course suitable for the work.

In a common sequel to disoriented fanning, the male settles near the female. He may be beside her, back of her or, most frequently, facing her. He then extends the proboscis, sometimes uncoiling and coiling it repeatedly and with speed and force; when uncoiled it often touches or even palpates the female's head, thorax, legs or, rarely, abdomen (Crane, 1955, Pl. III, Figs. 13-14).

Sometimes the male palpates similarly with his antennae. In these cases the proboscis is not uncoiled.

Once only a male *Dryas*, after prolonged disoriented fanning, settled obliquely to the side of the female, facing her, and alternately brushed each of his own eyes with the palp of the corresponding side. The motion was repeated several times and the performance was repeated an hour later.

Occasionally a period of proboscis extension or antennal palpation will be followed by resumed disoriented fanning, and then a second period of the more extreme form of irrelevant behavior. Sometimes the male persists in alternate disoriented fanning and its sequels until he appears altogether exhausted and remains perched motionless nearby. At these times he cannot even be urged into flight by a sudden

close wave of the observer's hand. Under ordinary conditions such a gesture sends into the air even butterflies that are fully accustomed to moving human beings and insectary conditions.

Nine situations regularly elicit irrelevant behavior in courting males. As previously stated, an advanced stage of courtship must have been reached before irrelevant behavior begins.

1. Courting of an unmated female, four to eight hours after her emergence; that is, on the afternoon of her first day.

2. Courting of a young mated female. It is now certain that second matings in females are very rare, and are practically confined to individuals that have already reached egg-laying age and are being persistently courted by young males in the absence of young unmated females.

3. Courting of a mated female about to lay eggs.

4. Courting of a male on his first or second day.

5. Courting of a very young imago of either sex, belonging to another species.

6. Loss of an unmated female, during courtship, through her flying out of sight.

7. Courting of females, unmated or mated, more than three days old by males more than about one month old.

8. Overcrowding of the insectary. This results in somewhat indiscriminate courting activity, apparently clearly attributable to the operation of the principle of heterogeneous summation and resulting in the courting of unsuitable individuals.

9. Unresponsiveness of unmated young females, or other failure in the final stages of courtship, due to unknown causes.

B. Females. Equivalent irrelevant behavior of females following broken-off courtships has not been detected. However, later in life a female's resistance to courtship appears to change in character to such an extent that it may be termed irrelevant behavior.

A recrudescence of courtship of egg-laying females is usual in all species. Very rarely these attempts end in copulation. The usual procedure is for the male to chase the female when she is beginning to hover around the foodplant, and to try to force her to alight for the Sedentary Phase in the usual fashion. At these times the female, flying with increasing strength as she is freed of the weight of eggs, usually manages to duck out from under the flying male and fly well above him. Then, instead of flying away as unresponsive younger females do, she hovers, mounting higher as he in turn tries to come on top. As

she grows older her flight above him more and more resembles the swift, vigorous flight of the fanning male, in which the fore- and hindwings are well separated (whether or not the friction surfaces in the species concerned hold the scent scales). The male usually soon gives up and flies away, without irrelevant behavior (see p. 139).

As the female grows older she chases passing butterflies with increasing frequency, regardless of their age or sex. Some chasing of other species, either related or of similar size and color, also occurs. This behavior continues even after egg-laying has ceased and, at least in *H. erato*, is strongest in those females that have completely finished egg-laying; in that species no eggs are laid after the age of about six weeks, while the female's imaginal life often extends to more than three months. Only in the last two weeks of life does this energetic chasing decrease.

The following special behavior has been observed only in females of *H. sara*. It occurs only on the two days preceding their first egg-laying or, alternatively, when another female has already laid on the only available space. (This species in Trinidad lays eggs in a cluster on the terminal leaflets of *Passiflora auriculata*). On these occasions *sara* uncoils the proboscis and with it touches either the spot on which she would normally lay, or the eggs already laid by another female. This procedure never occurs when she is actually ready to lay her own eggs, or when no other eggs are already in place.

VII. DISCUSSION

A number of points which have emerged from the observations described in the preceding pages now require comment.

It is clear that, in this group of butterflies, there can be no accurate description of courtship or other social behavior that is based on a few observations and individuals, any more than this is possible in the case of a higher vertebrate. The ages and past experience of each butterfly observed, particularly females, must be known in order properly to describe and evaluate their activities.

A. AGE. As in many birds, the patterns of reproductive behavior are not closely linked with successful reproduction. In the first place, the full specific courtship pattern is unnecessary for copulation. Before pairing with first-day females, males omit all except Stage III of the Second (Sedentary) Phase of courtship, and the youngest females gives no overt responses at all. These exceedingly simple courtships, in which practically all appetitive behavior is almost always

omitted, seem to depend predominantly on female scent, as do courtships in moths. All specific differentiation shows in courting females later in the first afternoon and, particularly, on the second or third days. Beyond that age, unmated females are receptive for at least three to six days, although their characteristic actions decline in both intensity and specialization.

Courting of very young males by other males, or of young individuals of other species, is undoubtedly due to the strong family odor of recently emerged insects. It is interesting that this odor apparently does not develop until the insect is at least ten minutes out of the chrysalid. Once a male *H. sara* actually copulated with a female *H. melpomene* when the latter, aged about one hour, was still unable to fly. Usually these two species, which are strikingly different both in color and, even to the human sense, in odor, have very little attraction for each other.

It is unlikely that females, which spend the first day practically inactive, are often found by males during these early hours. Odor alone is not an adequate releaser. A male, after losing sight of a newly alighted young female that has slipped underneath a leaf, sometimes searches around with every appearance of vagueness and inefficiency, and only rarely locates her once again.

B. SOCIAL CHASING AND RELATED TOPICS. It now seems clear that all the activities referred to in the paper on *H. erato* (Crane, 1955) as "social chasing" are appetitive fragments of the courtship pattern. They correspond to instances in numerous other animals where, as in frogs, a male in response to an incomplete stimulus situation embraces another male and, in the absence of appropriate response, releases his grip.

It is possible that in the wild some species of heliconiids maintain territories. All that can be said now is that in this family no trace of territorial behavior, or of a dominance hierarchy, has been observed either in the insectaries or during field observations. There is no patrolling of definite routes, no special display that lends itself to an interpretation of threat behavior, no overt fighting, no individual that usually is the pursuer in the frequent inter-male chases. On the other hand all of the chases of one male by another can be explained satisfactorily as merely the chasing phase of normal courtship which, because of the inadequacy of the sexual situation, breaks down. The break usually occurs after more or less mutual circling, which exactly resembles the circling resulting from the evasion attempts of unresponsive females (p. 138). When two males are courting the same female,

the latter often escapes in the general excitement and the two males continue for a short time chasing and fanning each other. Even when, through the breakdown of the releaser sequence, they "discover" the mistake there is no evidence of agonistic behavior; the two simply separate and go their ways. Rarely one or both of the males may continue rapid flight, apparently of an irrelevant character (p. 139).

It seems likely that the phylogenetic origin of gregarious roosting was the continuation of social chasing until time to hang up for the night. This could have become fixed, through the action of natural selection, into the stereotyped patterns of the species, as it came to have protective value. Presumably the strong species odors, which laboratory tests show to be unpleasant to predators, become intensified through crowding and could be a strong deterrent to nocturnal enemies that depend largely on the sense of smell. These enemies are probably chiefly reptiles and small mammals.

The increase of chasing by older females is of particular interest. This masculine type of activity would, in a vertebrate, be subject to a hormonal interpretation, in which the decline of female reproductive hormones leads to visible effects of male hormone activity. However, in insects, morphological sexual characters, at least, are not glandularly controlled; rather "... the sex of every part is controlled directly by the chromosome constitution of the cells composing it. Hence the sexual characters are unaffected by the removal of the ovary or the testes or even by their transplantation" (Ford, 1945, p. 192). Schneirla (1953, pp. 677-678), after citing references concerning mating behavior in insects that were castrated or otherwise sexually abnormal, commented, "Such results suggest that factors governing susceptibility in male and female insects are not directly dependent upon testes or ovaries, but may concern hormones already in the blood . . . the activity of some cephalic endocrine secretion, or other physiological agencies such as neural processes." The present instance, therefore, of pseudo-masculine behavior in aged female butterflies, is one more instance of the desirability of cooperative studies between physiologists and students of behavior.

C. IRRELEVANT BEHAVIOR. Irrelevant behavior proves to play a large part in the apparently normal social life of all butterflies under observation. It is not confined to species in captivity, since it has also been frequently observed in the wild. In fact, if only a few pairs of butterflies of a given species are observed in the Sedentary Phase in the field, it is far more likely that the

observer witnesses irrelevant behavior of some kind than a specifically characteristic courtship.

The various phases of irrelevant behavior and the situations which produce it have proved to be similar in all six species. In males, it is known certainly to take place only following an advanced stage of an incomplete courtship that is directed toward an unsuitable individual. It occurs in females after their most receptive period (see preceding section). Experiments to determine whether irrelevant behavior takes place in hungry individuals that are prevented from reaching visible and olfactorily detectable food have so far been inconclusive.

The instances of irrelevant behavior described are in completely different categories from "social chasing" since they are in no sense merely unfinished portions of the regular reproductive or roosting patterns. Like "social chasing," however, they never end in copulation.

Two of them, irrelevant proboscis-uncoiling and excessive, rapid, undirected flight, can appropriately be termed displacement activities. Occurring when the strongly activated sex drive is denied expression through its own consummatory act, the motions are clearly associated with other patterns of behavior, namely feeding and flight.

The once-observed eye-rubbing with the palps may be equivalent to the apparently displaced cleaning motions described in mantids (Crane, 1952), *Drosophila* (Bastock & Manning, 1955) and ocypodid crabs (Crane, 1957).

The two remaining types of irrelevant behavior in courting male heliconiids cannot be further classified at present. They should not, it seems, be termed displacement activities in the restricted sense (p. 136) since they do not occur in other behavior patterns found within the species. These motions are disoriented fanning and palpation of the female with the antennae. It may be, of course, that this palpation with the antennae, as well as with the proboscis, produces chemotactic sensations in a situation where the usual olfactory stimuli from the female are likely to be weak or incomplete. In the European satyrid, *Eumenis semele*, movements of the antennae form an integral part of courtship (Tinbergen *et al.*, 1943).

Disoriented fanning, in which the male may face in any direction with respect to the female, appears to be a disintegration of the normal pattern, resulting from a breakdown in the usual sequence of male-female responses. Subsequently the pattern often collapses altogether, the remaining energy being channelled into displacement-feeding or displacement-flight.

In all irrelevant behavior appearing during courtship, the non-responsiveness of the female, for whatever reason, appears to be the major factor. Males that are not in a physiological condition to complete courtship simply break it off at an early stage.

As stated in earlier pages, it is now certain that females normally mate only once. Each develops a specifically characteristic odor, given off by the abdominal glands, which becomes apparent to the human observer about an hour or more after the butterflies have separated. It is the same odor given off by mated females when seized. It seems likely that it is one of the deterrents leading to irrelevant behavior when males court mated females and do not follow through to copulation even though the females are making, to the human eye, all the visible responses characteristic of the species. Another deterrent in such cases seems to be the failure of the female to fold the wings, which have been more or less flattened during the courtship fluttering, above her back when the male alights beside her in Stage III. It is impossible for him to reach her abdomen with his harpes so long as her wings are flattened.

Use of the proboscis by *H. sara*, when egg-laying is apparently thwarted, is no part of the normal egg-laying procedure of any of the members of the family that have been studied, and perhaps should be termed displacement behavior. Unlike members of some other families (Ilse, 1955 and refs.), none of the heliconiids drum the foodplant with their feet before laying.

Finally, it may be re-emphasized that almost all these types of irrelevant behavior occur in the lives of all individuals of the appropriate sexes and ages that have been studied. No reliable interspecific differences have yet been observed.

VIII. SUMMARY

Six species of heliconiid butterflies from Trinidad, B.W.I., were reared in the laboratory and their post-emergence behavior studied in insectaries. Their social behavior patterns are briefly compared.

Social responses, including courtship, vary with age. In females the full courtship pattern is elicited only on the second and third days, although they can mate successfully when both younger and older. Younger females not only give little or no overt response but draw scarcely any pre-copulatory behavior from males. Older females show progressively fewer specifically characteristic responses.

Brief chasing of males or unreceptive females by males of any age and by old females is a com-

mon form of activity. It apparently represents simply a fragment of the appetitive portion of the courtship pattern. Neither territorial defense nor inter-male threat behavior seems to be involved.

Irrelevant actions of a number of kinds are frequent. Most occur in males that are thwarted, usually by the unresponsiveness of the female, after an advanced stage of courtship has been reached. Two kinds of irrelevant actions, a dis-oriented type of wing-fanning and palpation with the antennae, are not known in any normal behavior pattern of the species. Other types of irrelevant behavior appear to be true displacement activities, since they occur as appropriate actions in other fields of the insects' behavior, such as in feeding and flight.

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EXPLANATION OF THE PLATE

PLATE I

Figs. 1-6, incl. Species and subspecies of butterflies discussed in this contribution. Photograph by Sam Dunton, New York Zoological Society.

- FIG. 1. *Dryas julia julia*. General color: Orange.
- FIG. 2. *Heliconius melpomene euryades*. General color: Black; forewing band scarlet.
- FIG. 3. *Heliconius erato hydara*. Color as in *H. melpomene*.
- FIG. 4. *Heliconius ricini insulana*. General color: Black; forewing bands pale yellow; central portion of hindwing scarlet.
- FIG. 5. *Heliconius isabella isabella*. General color: Reddish - brown to yellowish - brown; marked with black.

- FIG. 6. *Heliconius sara rhea*. General color: Black; forewing bands pale yellow; basal half of hindwing with dark blue iridescence.
- FIG. 7. Irrelevant courtship behavior in *Dryas julia*: Sedentary phase, Stage II, showing poor orientation in fanning. In normal fanning the flying male faces in exactly the same direction as the sedentary female (Table II and p. 138). Note that female has forewings almost closed as required in Stage III. However, the hindwings are still fluttering, as is characteristic of earlier courtship stages, but atypical here. Photograph by M. Woodbridge Williams, © National Geographic Society.
- FIG. 8. Irrelevant courting behavior in *Heliconius erato*, corresponding to stage shown in Fig. 7. Photograph by Rosemary Kenedy.

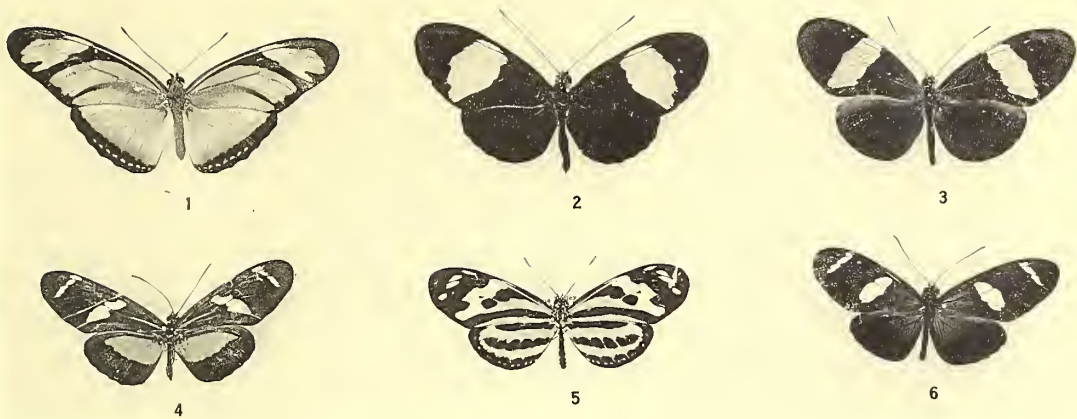


FIG. 7



FIG. 8

Habits, Palatability and Mimicry in Thirteen Ctenuchid Moth Species from Trinidad, B.W.I.¹

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(Plates I & II)

[This paper is one of a series emanating from the tropical Field Station of the New York Zoological Society, at Simla, Arima Valley, Trinidad, British West Indies. The Station was founded in 1950 by the Zoological Society's Department of Tropical Research, under the direction of Dr. William Beebe. It comprises 200 acres in the middle of the Northern Range, which includes large stretches of undisturbed government forest reserves. The laboratory of the Station is intended for research in tropical ecology and in animal behavior. The altitude of the research area is 500 to 1,800 feet, with an annual rainfall of more than 100 inches.

[For further ecological details of meteorology and biotic zones see "Introduction to the Ecology of the Arima Valley, Trinidad, B. W. I.," William Beebe. (Zoologica, 1952, Vol. 37, No. 13, pp. 157-184.)]

I. INTRODUCTION

THE highly specialized moths of the family known as the Ctenuchidae (Syntomidae, Amatidae, Euchromiidae) are among the most interesting and colorful of the Lepidoptera. In general, they are medium to small in size; many are brightly colored, some with metallic luster on wings and abdomen. More than 2,000 species are known, the great majority being restricted to the American tropics. Although they are commonly referred to as "day-flying" moths, many species fly also, or even exclusively, at night. Some species "mimic" other insects, and the larvae of some show remarkable adaptations (see especially Beebe, 1953).

The taxonomy of this group in Trinidad has been discussed by Kaye & Lamont (1927) and Fleming (1957), but relatively few observations have been reported on these moths in life: flight pattern, position at rest, frequency, time of flight and seasonal occurrence. Also, although it is well known that this family includes species which are obvious wasp and beetle "mimics," little experimental work has been done on the palatability of these moths to possible predators.

For this paper field observations and palatability tests were limited to 13 of the more than 80 species so far recorded in Trinidad. The choice of species was based on the following criteria: most are relatively common, therefore more readily available for observation and collection; they include both day- and night-flying species; they include genera from the most high-

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¹Contribution No. 980, Department of Tropical Research, New York Zoological Society.

ly specialized (*Pseudosphex*) to the most generalized (*Eucereon*, *Ctenucha*); they include species which show great differences in wing scaling, i.e., completely hyaline (*Pseudosphex*), completely scaled and having bright patches of color (*Histiata*), cryptic fuscous (*Episcepsis*) and metallic lustrous (*Macrocneme*); some species which are obvious "mimics" are included, and some which are drawn to *Heliotropium indicum* and others which apparently are not attracted to it.

This attractant is reported in detail by Beebe (1955 and refs.) but a brief summary is pertinent here. *Heliotropium indicum* Linnaeus is a common weed which, when uprooted and allowed to shrivel, exercises a remarkable selective attraction for several lepidopteran families including the Ctenuchidae. For some unknown reason, however, only certain species appear to be attracted to it, while other species common in the same locality ignore it completely.

The authors are indebted to Mr. Henry Fleming for identification and range of the ctenuchid species used in this study.

II. MATERIAL AND METHODS

Nearly all observations and collections were made within a radius of approximately a quarter of a mile from the Simla field station, the majority within 100 yards of the laboratory. At night they were made at several incandescent electric light bulbs outdoors and at a spotlighted sheet, by day along trails, roadside or in the laboratory itself where a large screened window trapped many of the day-flyers which entered at an open end of the room. *H. indicum* was used both night and day as a collecting and observing site. The best results were had with this attractant when a clump of the weed was suspended from a low tree branch along a shaded trace.

Abundance records used in this paper were kept during the three-year period 1953-1955 but cover only the months of December to June, the extreme limits of our stay at the field station.

Rest position was usually observed on a captured uninjured moth placed in a large glass jar or terrarium. Most flight observations were made on free-flying moths at night lights or at *H. indicum*, or inside a screened insectary measuring 12 × 18 feet.

As shown in Table 1, the relative acceptability of moths to various vertebrates and invertebrates was tested. In experiments with ants, the ctenuchids were either freshly dead or completely incapacitated. No chemicals were used for killing. With all the other testers, living active specimens

were used. There is an occasional record of a mantid or a spider capturing a ctenuchid in the field, but all experiments with bird, lizards, frog, tarantula and with most mantids were done with the testers in captivity. The *Polychrus* lizard and the bird, a Moriche Oriole, were tamed specimens which readily accepted food held by forces in the hand.

In each test, with the exceptions just mentioned, an active moth was placed in the terrarium or cage with the tester and the response of the latter was noted. Each test was controlled, i.e., a negative result was listed only if another lepidopteran specimen, usually a pyralid moth or a riodinid butterfly of comparable size, was accepted immediately afterwards.

The results of the tests were classified as follows:

A—Moth eaten entirely (with occasionally the obvious exception of wings or genitalia).

B—Moth eaten partially or with apparent distaste, i.e., mouthed (by bird or mantid), sucked for short time (spider), partially eaten only (ants, mantid, bird), or eaten with apparent distaste (frog).

C—Moth originally noticed (antennae or dragged by ants, seized by mantid, spider, frog, lizard or bird) but eventually released without being injured.

D—Moth ignored completely or fled from.

The numeral following each of the above classifications in Table 1 indicates the number of tests performed with that result.

III. OBSERVATION AND RESULTS

Pseudosphex kenedyae Fleming
(Plate I, Figure 1; Plate II, Figure 14)

Range.—Trinidad.

Field Name.—Dusky-winged Wasp-mimic.

Field Characters.—Thorax yellow with dark brown markings; abdomen yellow banded with brown, constricted at base; wings hyaline with fuscous streak along costal margin of forewing. In flight, cannot be distinguished from another Trinidad ctenuchid, *Sphecosoma trinitatis* Rothschild, nor from its vespid wasp "models" (see below). Sexes differ by presence of ventral valve in ♂.

Frequency.—This species was not seen by us until dead *Heliotropium indicum* was used as an attractant. Since then it has been very common on the weed. The attraction is almost limited to ♂♂, as out of 114 individuals seen or taken, only one was ♀.

Active Period.—One of the most decidedly

TABLE 1. PALATABILITY OF CTENUCHID MOTHS

Explanation: A—eaten completely
B—eaten partially or with distaste
C—uneaten, but originally noticed
D—ignored

The numeral following each of the above categories indicates the number of tests performed.
For further details, see "Material and Methods."

Species of Ctenuchid Moth														
Palatability Testers	<i>Pseudosphex kenedyae</i>	<i>Saurita clusia</i>	<i>Histiata cepheus</i>	<i>Macroceme thyra intocta</i>	<i>Calonotus craneae</i>	<i>Aethria carnicauda</i>	<i>Episcepsis hypoleuca</i>	<i>Napata wolkeri</i>	<i>Agryta duz</i>	<i>Eucereon mota</i>	<i>Eucereon obscurum</i>	<i>Correbidia assimilis</i>	<i>Ctenucha andrei</i>	
Ants <i>Monomorium floricola</i> <i>Ectein vagans</i> <i>Dolichoderus hispinosus</i>	C1, D2 C1, D2 D5	B1, D3 A2	D1 C2, D1 B2, C4, D2	D11 D1 D2	B2, D2	A1, B4, D3 C1 D7	B2, D1 A1, B1, D5	 A1	A2 B1	B5 A2, D5	B1	B1, D2 B1 A1	A1, D2 B1, D1 A2, B2, D1	
Mantids <i>Stagmatoptera septentrionalis</i> <i>Votes lobola</i> <i>Acanthops falcata</i> <i>Oxyopsis rubicunda</i> <i>Stagmomantis carolina</i> <i>Thesprotio filum</i>		A2 A2 A1	B1, D2 B1 B1	C2, D2 A1, B1, C1 A1 A4, B2 B1	A1 A2		A1 A1				A1	A1, B1 A1	A1	
Spiders <i>Tarantula</i> <i>Epeirid</i> <i>Argiope</i> sp.		B1, C1	C2, D2	B1, C4 D2	C1					A1 A2		A1	A2	
Frog <i>Hyla morima</i>		A1, B2	A1, D1	A2, C1, D3	C1, D1		A1, C1			A2, B1, C4, D1	A1	A1	A1	
Lizards <i>Polychrus marmoratus</i> <i>Thecadactylus rapicaudus</i>	D1		A1, C5, D4	A2, D1 D2			D1					A4, D1	A4	
Bird <i>Icterus chrysiocephalus</i>	C5, D5	D2	B1	D5	D1	D1	C1, D2		C2	A1, B2	B1, C4	C1, D3	C2, D4	
Totals, Degree of Palatability	C7, D15	A8, B4 C1, D5	A2, B6 C13, D13	A10, B5 C8, D29	A3, B2 C2, D4	A1, B4 C1, D11	A4, B3 C2, D9	A1	A2, B1 C2	A8, B8 C4, D6	A3, B3 C4	A10, B3 C1, D7	A11, B3 C2, D8	
Total Tests Made	22	18	34	52	11	17	18	1	5	26	10	21	24	

diurnal of the ctenuchids, flying, often with its model, from early morning (6:00 to 6:15 A.M.) to nearly dusk. In a terrarium it is invariably positively phototropic. Observed every month from December to June.

Rest Position.—Wings 75° back, at times vertical. When walking, wings 45° back, 45° up. Antennae in constant motion, often alternately. When pausing between steps, the abdomen is frequently twitched up and down several times.

Flight.—Quick, jerky darts, wholly wasplike; sometimes remains suspended before landing, motionless except for the wings, the hindlegs extended downward and slightly backward. It has been seen to alight directly on the underside of a leaf without any hesitation and without alighting on the upperside first.

Palatability.—(Table 1). In every one of the 22 tests made, this species proved to be unacceptable to lizard, bird and three species of ants. In 15 tests the moth was ignored completely; in only seven cases was it approached or noticed. Army ants dragged a living moth by one leg for a few seconds before releasing it, uninjured. In another instance, ants approached a freshly dead specimen, touched it with their antennae for a short time but ignored it thereafter. In five tests the tame Moriche Oriole started to approach a living moth but backed away almost immediately; in one case it pecked at the forceps but not at the insect held by it. In five other tests with the same bird the moth was ignored completely.

Mimicry.—There exists a remarkably exact resemblance between this day-flying moth and several of the common Simla wasps. In our first search for this mimicry we captured seven of the wasps and a single ctenuchid. The latter was resting head down on a dry leaf of *Heliotropium indicum*, while the former were either flying or resting on leaves or inside the laboratory. This particular hymenopteran was *Stelopolybia pallipes* var. *anceps* (Saussure).

The two field characters by which the "model" and "mimic" may best be distinguished are the head, that of the wasp being wider and bearing a pair of jaws rather than a proboscis, and secondly, the antennae. The solidity of the antennae in the case of the wasp or the pectination in the case of the moth is made more difficult for differentiation by the fact that in the moth the pectination comes to an abrupt ending about two-thirds from the base, the distal end being reduced to a slender, easily overlooked filament.

Other insects bearing a close resemblance to this moth are *Oriodes* in Syrphidae and one of the Stratiomyidae, both dipterans.

The force of the mimicry is enhanced by the following characters: *Size*: In total length the wasp is 12 mm., the moth 10 mm. *Shape*: The abdomen of the moth is proximally constricted to a most unmothlike degree. *Color and Pattern*: Basic amber color the same, also the thoracic and abdominal pattern. *Antennae*: Nervous twiddling. *Walk and Flight*: Character, speed and details of manoeuvrability similar in moth and wasp. When the moth is feeding, its abdomen is lifted into a curve and occasionally raised and lowered, emphasizing the wasplike shape and pattern. *Wings*: As in the wasp, the wings are held 45° up and out, and the costal area is darker than the remainder of the forewing. Another remarkable wing character was noted by Kaye (1913) in *Pseudosphex* spp. He observed that they "curve the forewing while the hindwing is folded up, so that the wings appear to be as narrow as the completely folded wings of the Vespidae and Eumenidae." This character applies also to the Trinidad species, and is shown to some extent in Plate II, figure 14.

On the whole, the present species of ctenuchid appears to offer an almost perfect example of Müllerian mimicry: the moth is definitely distasteful, and its extremely close hymenopteran counterpart possesses an efficient sting.

Saurita clusia (Druce)

(Plate I, Figure 2)

Range.—French Guiana and the Amazon Region.

Field Name.—Black-tipped Whitewing.

Field Characters.—Wings yellowish-white, dusky at base with large apical spot. Five red spots, paired on shoulders and collar and one at base of dorsal abdomen. Hindwings short and rounded. ♀♀ with more extensive black scaling at apex and base of forewing and antennae less heavily pectinated, almost threadlike.

Frequency.—One of the most common species at Simla, but of the 156 individuals seen or taken, only five have been ♀♀.

Active Period.—Strictly nocturnal. Taken every month, December to June.

Rest Position.—Wings 60° back, flat, tips clear of surface. When walking the wings are raised 45° and held well apart. Thorax and narrow anterior segment of abdomen exposed, revealing the five scarlet spots. Antennae 45° apart.

Flight.—At first, forewings are waved slowly, then all four are whirled, before taking off. Flight is flylike, usually more or less straight upward, the insect finally alighting and walking at once. When liberated from a hand-held con-

tainer in an insectary, the moth seeks shelter beneath fingers or in a dark crevice in the rafters, as if to avoid the light. Twice found resting beneath a leaf.

Palatability.—(Table 1). This species appears to be acceptable to mantids, moderately so to spider and frog. A specimen was seized by a tarantula but immediately released; later the same specimen was captured and the abdomen sucked for several minutes, but it was eventually released alive and able to walk. Two specimens were eaten by frog with apparent distaste. Two were refused by Moriche Oriole. But as the moth is strictly nocturnal, these negative results with the bird appear to have little or no survival value.

Mimicry.—No definite models have been observed in association with this species. It is flylike in many respects but is strictly nocturnal.

Histiæa cepheus (Cramer)

(Plate I, Figure 3)

Range.—Venezuela to Surinam.

Field Name.—Large Red-and-yellow-spotted Brown.

Field Characters.—Large (expanse $2\frac{1}{2}$ inches), dark brown; forewings with three buffy yellow spots, hindwings with two large, irregular, scarlet spots; basal segments of dorsum with three incomplete yellow bands. Sexes very similar; abdomen of ♀ slightly broader.

Frequency.—Common. Of 81 moths seen or taken, two-thirds were ♂♂.

Active Period.—Strictly nocturnal, usually taken at lights before 10 P. M. Twelve imagoes, reared from larvae (Kenedy, unpub.), were placed in an insectary for observation. They were inactive during the day, usually resting, singly, beneath a large leaf. From 6:00 to 6:30 P.M. they began to be active, flying and walking on the screening of the roof. Seen or taken all months, December to June.

Rest Position.—Wings 50° back, tips not touching surface. Abdominal bands exposed. The moth has often been observed to wave its wings up and down, through a rather large arc, when standing still or walking, or to whirr its wings rapidly.

Flight.—In an insectary, it took off with moth-like flight, the slow beat of the wings rendering them visible. Liberated in the open, it rose swiftly and smoothly, circled twice in mid-air, then flew straight over the valley.

Palatability.—(Table 1). Thirty-four tests were completed, 26 of which demonstrated that this species could be considered unpalatable. A rather unique phenomenon has been observed

in this species. When a specimen is immobilized suddenly, whether captured by a caged tester such as a mantid or held by observer, it has been seen in many cases to exude droplets of thick yellow fluid from the thorax. Sometimes the droplets are bubbly and almost completely cover the dorsal thorax. This seems to serve as an effective defense against at least some predators. In two cases mantids bit into the dorsum but dropped the moth when the yellow froth came in contact with their eyes and mouthparts; a lizard five times threw a captured but uninjured insect from its mouth with violent shaking of its head. In the single test with the Moriche Oriole it ate the interior of the thorax and abdomen, leaving the head, genitalia and entire exoskeleton. In this case, no drops of fluid were observed on the insect's thorax. A tarantula ignored two specimens, and captured but immediately released two others undamaged.

Macrocneme thyra intacta Draudt

(Plate I, Figure 4; Plate II, Figure 15)

Range.—Trinidad and Colombia.

Field Name.—White-bellied Greenwing.

Field Characters.—Wings black, basal half with metallic blue-green sheen; dorsal base of abdomen with four white spots; hind tarsi white tipped; ♂ white below on thorax and abdomen, ♀ venter with white spots.

Frequency.—Abundant. ♂♂ dominate in number: of 326 seen or taken, only 10 were ♀♀.

Active Period.—Chiefly night flyers. Of 326 individuals, 14 (nine ♂♂, five ♀♀) were netted by day. Seen or taken every month, December to June.

Rest Position.—Wings 20° back, flat, the forewings overlapping the hindwings so that the latter are invisible. Antennae 45° apart. When walking, movements are nervous and jerky, wasplike; wings held up and back 30° to 45° ; antennae in motion.

Flight.—Wasplike, direct. The long hindlegs are held down and backward in flight. When several captured ♂♂ were released they spiralled upward fairly slowly or circled several times before flying away. Half of the total ♀♀ collected were netted while they were flying slowly along roadside or near stream, in bright sunshine.

Palatability.—(Table 1). Fifty-two tests were made with this species. In 29 the moths were ignored completely and in eight they were originally noticed but uneaten. In five tests with the Moriche Oriole, the bird would not approach the insect; in one case the bird appeared to jump agitatedly around its cage during the several

minutes the moth was crawling inside. Ants ignored freshly dead specimens in all 14 tests. Mantids, however, ate 75 per cent. of the specimens offered to them, and frog and *Polychrus* lizard occasionally accepted the moths.

Mimicry.—As noted by Kaye (1913), members of the genus *Macrocneme* seem to be excellent mimics of fossorial or pompilid wasps, especially the genera *Salix* and *Pepsis*. *M. thyra intacta* is wasplike both in facies and in behavior. The wings and abdomen possess a metallic blue-green sheen; the long hindlegs, more heavily scaled than is usual in ctenuchids, are extended downward and backward in flight. Kaye also noted that they wave their antennae and vibrate their wings rapidly when alighted, and that they settle usually, like fossorial wasps, on ground, bank or leaf.

Calonotos craneae Fleming

(Plate I, Figure 5)

Range.—Trinidad.

Field Name.—White-spotted Green-stripe.

Field Characters.—Wings black, with two or three white spots on forewing (♂♂ have two and sometimes a smaller third; ♀♀ have three); a single spot on hindwing; abdomen black with three longitudinal, iridescent, pale green stripes.

Frequency.—Common, 78 having been recorded or collected, with ♀♀ slightly outnumbering ♂♂.

Active Period.—This species has been taken at Simla only at night lights, chiefly before 10 P.M. However, one specimen was captured by Fleming in central Trinidad in daytime, in palm and immortelle forest. Have been taken December to June, with March, April and May the time of heaviest flight.

Rest Position.—Wings 50° back, 30° raised. Hindwings concealed. Black abdomen exposed, showing conspicuous streaking of iridescent green. Antennae 45° up and out.

Flight.—Relatively slow, direct. On one occasion at night light a moth was seen to "play dead" when taken.

Palatability.—(Table 1). Specimens refused or rejected by bird, frog and tarantula. Ants ate interior of two moths, ignored two others. Eaten by mantids.

Aethria carnicauda (Butler)

(Plate I, Figure 6)

Range.—Venezuela and Brazil.

Field Name.—Red-tailed Clearwing.

Field Characters.—Black with red-tipped abdomen; wings hyaline with margins and veins

black. ♂♂ with palpi, shoulder spot, forecoxae and ventral base of abdomen white; ♀♀ lack white. This species may be mistaken for *Dinia mena* (Hübner) but the latter has the scarlet abdominal fringe extended well up the sides.

Frequency.—A common species; 66 were observed or collected; ♀♀ slightly outnumbered ♂♂.

Active Period.—Confined to daylight, from 8:30 A.M. to 4:30 P.M. Observed from December to June. The moths are more numerous at the end of the dry season, in March and April.

Rest Position.—Wings 60° back, flat, inner edges not quite touching. In walking the wings are raised 40°, spread so that the hindwings are exposed; wings in slight but constant motion. When the moth is walking about on the attractant *H. indicum* the antennae are constantly in play, tapping the surface.

Flight.—Apparently more swift and direct than is usual in the group. A moth liberated five times in an insectary flew straight upward toward the light.

Palatability.—(Table 1). This species was tested with ants and bird only. Refused in single test with Moriche Oriole; ants ate five of 16 specimens.

Episcepsis hypoleuca Hampson

(Plate I, Figure 7)

Range.—Central America.

Field Name.—Red-collared Brownwing.

Field Characters.—Wings unicolored snuff brown; forecoxae red; dorsal abdomen metallic blue. ♂♂ with white at base of ventral abdomen.

Frequency.—Common. Total recorded 128, of which 82 were ♂♂, 34 ♀♀ and 12 undetermined.

Active Period.—Chiefly nocturnal, both at lights and *H. indicum*. Approximately 20 per cent. were taken in the daytime; the sex ratio remained constant. Seen December to May, with heaviest flight in December and January.

Rest Position.—Wings 70° back, not touching surface, overlapping at anal angle, meeting medially.

Flight.—Slow, slightly wavering until full speed is attained, then direct, not very rapid. Fairly sluggish on *H. indicum*, crawling slowly in and out of dried branches, sometimes dropping instead of flying off when approached.

Palatability.—(Table 1). Refused or rejected by bird in three tests, by house gecko in a single test; frog ate one, rejected another; eaten by mantids; ants ate four, ignored six.

Napata walkeri (Druce)

(Plate I, Figure 8; Plate II, Figure 16)

Range.—Mexico, Central America.

Field Name.—Barred-tip Yellow.

Field Characters.—Wings orange-yellow; apex of forewings white barred with black; palpi, legs and ventral surface black and white. Sexes indistinguishable in the field.

Frequency.—Taken occasionally at Simla. Of a total of 25 specimens, 22 were ♂♂, three ♀♀.

Active Period.—Nocturnal. Taken from December to June, with the exception of May.

Rest Position.—Wings 70° back, just meeting at midline over dorsum; tips not touching surface.

Flight.—Wavering and not rapid. At end of flight may seek shelter under leaf.

Palatability.—Because of the comparative rarity of this species, only one specimen was tested, and that inadvertently. It was a rare ♀ which was being kept in captivity in the hope of obtaining eggs. When freshly dead, ants swarmed over it and ate it before it could be salvaged for the collection.

Mimicry.—This orange-yellow ctenuchid is quite unlike other members of its family, but there are several species of other families which in color and pattern might be considered as models. Among these are the riodinid butterfly, *Mesene semiradiata*, and the zygaenid moth, *Malthaca radialis*. A pyralid moth, *Mapeta xanthomelas*, fulfills all the demands in numbers and appearance of a model, although it is a day-flying species. At rest the ctenuchid and the pyralid are remarkably similar, and not until one is close enough to see the backward angle of the antennae and the prominent palpi of the pyralid can they be distinguished (see Plate II, fig. 17). In flight, however, the barred hindwings of the pyralid are quite visible; the ctenuchid lacks these markings.

Two of the pyralids were tested for palatability with ants and were eaten except for the shell of the thorax. However, two specimens were ignored by the Moriche Oriole.

Agyrta dux (Walker)

(Plate I, Figure 9)

Range.—Central America to Venezuela and Brazil; St. Lucia.

Field Name.—Six-windowed Black.

Field Characters.—Relatively large moth, black shot with blue; wings with six large, irregular hyaline areas, two in forewing, one in hindwing, crossed by black veins; wing bases, thorax and abdomen iridescent blue; palpal base and tongue scarlet; narrow dorsal abdominal

streak and venter white. Sexes similar except for slightly shorter antennal pectinations in ♀. Differs from closely related *A. micilia* by hyaline forewing area arising near base.

Frequency.—Occasionally recorded at Simla. A total of 23 consisted of 19 ♂♂, three ♀♀ and one undetermined.

Active Period.—Exclusively diurnal, taken from early morning to late afternoon, with the majority seen in late afternoon. December and January have been the best months for recording this species, but they have also been taken in March, April and May.

Rest Position.—Wings 20° to 40° back, meeting over back. When walking, wings are waved through a 45° arc; antennae in constant motion, moving in unison.

Flight.—Fairly rapid, darting, low, circling before alighting. It was seen to alight on dead *H. indicum* three times at the same spot. At once it began to search eagerly with its tongue, within a small area. After feeding on a panicle it literally ran through the dense, dry foliage, its wings rubbing against the leaves in the narrow places. Its speed was remarkable in the deeper interstices. The wing iridescence and the deep red collar and tongue could be plainly seen when the rest of the insect was invisible.

Palatability.—(Table 1). This species is apparently palatable to ants. A small ponerine ant was once seen carrying off a ♀ specimen, holding it at the tip of the abdomen. The insect was rescued, but died. The Moriche Oriole twice picked up a specimen hesitantly, but dropped it without injury.

Mimicry.—An unidentified geometrid moth is a close model for the species except for its smaller size, spreading only 28 mm. whereas *A. dux* extends 40 mm. between wingtips. The rest position of the geometrid is similar to that of the ctenuchid and it also is a day-flyer. Both in facies and flight, *A. dux* appears more butterfly-like than is usual in the group.

Eucereon maia Druce

(Plate I, Figure 10)

Range.—Mexico, Central America, Venezuela, British Guiana.

Field Name.—Red-bodied Brown.

Field Characters.—Thorax and forewings light brown, mottled with darker; hindwings pale; abdomen red above, dotted with black, whitish below. Forewings of ♀ paler.

Frequency.—♂♂ of this species are abundant. Total of 260 seen or taken consisted of 196 ♂♂, 12 ♀♀ and 52 undetermined.

Active Period.—Nocturnal, flying throughout the night, appearing at dusk and seen also at dawn with records every hour to 3 A.M. The peak of the flight seems to be 10:30 to 11:30 P.M. In an insectary the moth is negatively phototropic. Recorded every month from December to June, with December and January the months of heaviest flight.

Rest Position.—Wings 70° back, overlapping, completely covering abdomen.

Flight.—Rapid and direct, occasionally circling once or twice. When disturbed, the moth often drops to the ground, beetlelike, before taking flight. Or it may crawl along the ground instead of flying, sometimes hiding under a low-growing leaf. The habit of dropping is so usual that a specimen can almost always be collected merely by placing the open end of a vial beneath it.

Palatability.—(Table 1). Ants ate seven specimens, ignored five; spiders sucked three; one was captured and eaten by a centipede on *H. indicum*. In majority of tests the frog captured but spit out this species. The Moriche Oriole ate one, ran two others through its bill, then flicked them away, injured.

Eucereon obscurum (Möschler)

(Plate I, Figure 11)

Range.—Mexico and Central America south to the Amazon.

Field Name.—Blue-spangled Bronzewing.

Field Characters.—Abdomen black, the terminal segments shot with blue; forewings bronze-black, faintly spangled and lined with bluish-white; hindwings semi-hyaline, pale brown. Sexes indistinguishable in the field.

Frequency.—A common species. Of 87 specimens 58 were ♂♂, 10 ♀♀ and 19 undetermined.

Active Period.—Exclusively nocturnal, like others of the genus. It first appears in early evening and has been found as late as 3:30 A.M. Has been taken from December to June, with the heaviest flight in December and February.

Rest Position.—Wings 80° back, almost parallel; inner edges overlapping, concealing body; tips resting on surface.

Flight.—A rapid fluttering, but rather slow flight. The moth circles slowly, hovers before alighting. When released in insectary, it invariably flew to the ground and hid among grass.

Palatability.—(Table 1). Eaten by ants, mantids and frog; Moriche Oriole ate head and thorax of one, seized four others but dropped them immediately.

Correbidia assimilis (Rothschild)

(Plate I, Figure 12; Plate II, Figures 18, 19)

Range.—Venezuela, British Guiana, Surinam, Brazil.

Field Name.—Yellow-banded Beetle Mimic.

Field Characters.—Small moth. Wings black, crossed in center by a wide, pale yellow band. Sexes indistinguishable in the field except by slightly shorter antennal pectinations in ♀.

Frequency.—The most abundant ctenuchid at Simla. Total recorded 337, of which 205 were ♂♂, 30 ♀♀ and 102 undetermined.

Active Period.—More than 95 per cent. were seen or taken at night, being drawn chiefly to lights but also to uprooted *H. indicum*. Occasionally taken during the day and then usually in the early morning or late afternoon, within two hours of dawn and dusk. Seen from December to May. The numbers drop off in April and May.

Rest Position.—Wings 80° back, outline curved, overlapping medially, only thorax exposed. In this position the light yellow midwing markings form a continuous transverse band. Antennae 45° forward and out, tips slightly curved. When walking the moth waves its antennae alternately up and down. This species appears to be unusually lethargic and slow to take flight.

Flight.—Slow and fluttering.

Palatability.—(Table 1). Ants ate three specimens, ignored two; eaten by mantids, spider, frog and lizard; Moriche Oriole ignored three, approached one hesitantly but would not take it.

Mimicry.—Several authors, especially Kaye (1913), have commented on the remarkable resemblance that exists between members of this genus and lycid beetles, such as the genus *Lycomorpha* in North America. Lycid beetles are general in the Neotropics and are known to be protected (Forbes, 1930, p. 27). There are three Simla insects which might be considered as models for *C. assimilis*: a small arctiid moth, *Lycomorphodes aracia*, and two lycid beetles, a smaller and a larger species (Plate II, figs. 18, 19). The arctiid and the smaller beetle are nocturnal, the larger beetle is a day-flyer.

The smaller lycid is common and frequently found associated with the ctenuchid. The larger beetle and *C. assimilis* are similar in color and pattern and in their slow, lethargic movements. They also resemble one another in appearance and movements of the antennae, and in the mutual habit of slowly lifting and lowering the forewings (elytra in the case of the beetle) as

they walk. The average in both is seven waves in five seconds.

During the same length of time 54 arctiids, 37 lycids and 130 specimens of the ctenuchid were recorded.

Kaye (1913) made several interesting observations on mimicry in *Correbidia* which we have also noted in *C. assimilis* in Trinidad: they are sluggish in the early morning and, beetlelike, drop to the ground when disturbed, drawing their legs in; the shape and color of wings are like a lycid beetle. To heighten the deception, the abdomen of the moth is slightly flattened, the legs are short and the heavy pectinations of the antennae are carried to the tip.

To check palatability, the two beetles and the arctiid were tested with ants. Three specimens of the arctiid were eaten; one large and two small beetles were untouched.

Ctenucha andrei Rothschild

(Plate I, Figure 13)

Range.—Has been recorded also from British Guiana.

Field Name.—Large White-banded Black.

Field Characters.—A good-sized moth; forewings blue-black with broad, oblique, white band; hindwings steel blue. ♂♂ with white on venter, ♀♀ black.

Frequency.—♂♂ common, ♀♀ rare. Of 89 specimens, 63 were ♂♂, 2 ♀♀ and 24 undetermined.

Active Period.—A diurnal species, flying at any hour of the day from dawn to dusk. A single exception was a ♂ taken at the night light in early evening. Observed from December to June.

Rest Position.—Wings 60° back, meeting over dorsum; white bands on forewings not meeting. When walking the moth waves its wings slowly through a 45° arc. Antennae 70° forward, 20° apart.

Flight.—Rather slow and fluttering. In flight the wings become a black haze, with curved ring of white above and below. Wings move through an arc of 130°.

Palatability.—(Table 1). This species was eaten by mantid, tarantula, frog and lizard. In 60 per cent. of the tests with ants the moth was eaten. Army ants ignored one specimen, killed but did not eat another. In two tests the Moriche Oriole took the moth but dropped it immediately; it ignored four others.

Mimicry.—The most reasonable "model" for this species is *Cecropterus bipunctatus* (Hesperiidae). In abundance, pattern and color, general motions and habitat this approximates the

ctenuchid. However, this skipper was found to be acceptable to the Moriche Oriole.

IV. DISCUSSION

Table 2 is a recapitulation of data, most of which are already given in the text under individual species, with the addition of positive or negative results with the use of *Heliotropium indicum* as an attractant. These results bring out several interesting problems: although the attraction of the weed is highly selective, being almost exclusively limited in the Heterocera to the family Ctenuchidae, yet some of the most common Trinidad ctenuchids, such as *Macrocne thyra intacta*, have never been found on it. *Pseudosphex kenedyae* is a common visitor to *H. indicum*, but it has not been seen elsewhere nor had we ever seen a specimen before using the attractant. Other ctenuchids are common both at lights and on the weed, such as *Correbidia assimilis* and *Eucereon maia*; however, another member of the same genus, *E. obscurum*, is fairly common at lights but extremely rare on *H. indicum*.

Frequency.—The species are listed in order of abundance in Table 2. The sex ratio of 11 species shows a predominance of males. However, females slightly outnumber males in *Calonotos craneae* and *Aethria carnicauda*. As the latter flies by day and as the larval foodplant is a low-growing sedge (see Beebe, 1953) and as eggs are laid singly (Kenedy, unpub.), it is perhaps reasonable to suppose that ovipositing females would be seen and netted more often than males. But in the case of *C. craneae* all the females seen or taken at Simla were attracted to night lights.

Active Period.—Six species were found to be exclusively nocturnal and four exclusively diurnal; three species were active both by day and at night, although chiefly nocturnal.

Rest Position.—The backward angle of forewings at rest ranges among the 13 species from 20° in *Macrocne thyra intacta* to an almost parallel 80° in *Eucereon obscurum* and *Correbidia assimilis*. The wasp "mimics," *M. thyra intacta* and *Pseudosphex kenedyae*, hold their wings at a slightly upward angle when walking; the other species hold them either parallel to the surface or angled slightly downward so that the apex is almost touching the surface.

Flight.—There is great variation in habits of flight, from slow and wavering (*Correbidia assimilis*, *Episcepsis hypoleuca*) to rapid and direct (*Aethria carnicauda*, *Eucereon maia*).

Palatability and Mimicry.—In Table 1 the results of palatability tests show that the only

TABLE 2. FREQUENCY, ACTIVE PERIOD AND ATTRACTION TO *Heliotropium indicum*

Species are listed in order of abundance. Totals are for three-year period 1953-1955, principally during January to April. Extreme limits of observation and collection were December to June.

Species	Frequency				Active Period		Attraction to <i>H. indicum</i>
	Total Seen or Taken	Sex Ratio			%	%	
		% ♂ ♂	% ♀ ♀	% Un- determined			
<i>Correbidia assimilis</i>	337	61	9	30	5	95	+
<i>Macrocneme thyra intacta</i>	326	97	3		4	96	—
<i>Eucereon maia</i>	260	75	5	20		100	+
<i>Saurita clusia</i>	156	97	3			100	—
<i>Episcepsis hypoleuca</i>	128	64	27	9	20	80	+
<i>Pseudosphex kenedyae</i>	114	> 99	< 1		100		+
<i>Ctenucha andrei</i>	89	71	2	27	100		+
<i>Eucereon obscurum</i>	87	67	11	22		100	+(rare)
<i>Histiaea cepheus</i>	81	68	22	10		100	—
<i>Calonotos cranaea</i>	78	45	49	6		100	—
<i>Aethria carnicauda</i>	66	45	55		100		+
<i>Napata walkeri</i>	25	88	12			100	+(rare)
<i>Agyrta dux</i>	23	83	13	4	100		+

species which appears to be well protected from potential enemies is the vespid wasp "mimic" *Pseudosphex kenedyae* and therefore is an excellent example of Müllerian mimicry. Although tests with the other species are inconclusive, it seems that they are at least partially protected against possible predators.

V. SUMMARY

Field characters, sex differences, frequency, active period, rest position and flight are recorded in 13 of the more common species of ctenuchid moths in Trinidad.

Interesting habits include extremely wasplike flight as well as facies in two species, and in two others a beetlelike dropping to the ground when disturbed.

In two species only, more females were seen or taken than males; in the others, males far outnumbered females.

There is great variation in habits of flight and in rest position among the 13 species.

Their palatability to various vertebrates and invertebrates was tested under controlled conditions. They appear to be at least partially unacceptable to possible predators.

It is suggested that a fluid exuded from the thorax of *Histiaea cepheus* serves as an effective defense.

Mimicry in several species is discussed. *Pseudosphex kenedyae* appears to be an almost perfect example of Müllerian mimicry.

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EXPLANATION OF THE PLATES

PLATE I

- FIG. 1. *Pseudosphex kenedyae*.
- FIG. 2. *Saurita clusia*.
- FIG. 3. *Histiaea cepheus*.
- FIG. 4. *Macrocneme thyra intacta*.
- FIG. 5. *Calonotos craneae*.
- FIG. 6. *Aethria carnicauda*.
- FIG. 7. *Episcepsis hypoleuca*.
- FIG. 8. *Napata walkeri*.
- FIG. 9. *Agyrta dux*.
- FIG. 10. *Eucereon maia*.
- FIG. 11. *Eucereon obscurum*.
- FIG. 12. *Correbidia assimilis*.
- FIG. 13. *Ctenucha andrei*.

PLATE II

All photographs are of living specimens in natural rest position, taken in a confined area.

- FIG. 14. *Pseudosphex kenedyae* feeding on *Heliotropium indicum* seed panicle. Note wasp-like pattern, constriction of abdomen and curve of forewings; also reduction of pectinations on distal third of antennae.
- FIG. 15. *Macrocneme thyra intacta*, showing long, heavily scaled hindlegs and white tarsi.
- FIG. 16. *Napata walkeri*.
- FIG. 17. *Mapeta xanthomelas* (Pyalidae).
- FIG. 18. *Correbidia assimilis* and small lycid beetle.
- FIG. 19. Same, with large lycid beetle.



FIG. 1



FIG. 2



FIG. 3



FIG. 4



FIG. 5



FIG. 6



FIG. 7



FIG. 8



FIG. 9



FIG. 10



FIG. 11



FIG. 12



FIG. 13

HABITS, PALATABILITY AND MIMICRY IN THIRTEEN CTENUCHID MOTH SPECIES FROM TRINIDAD, B.W.I.



FIG. 14

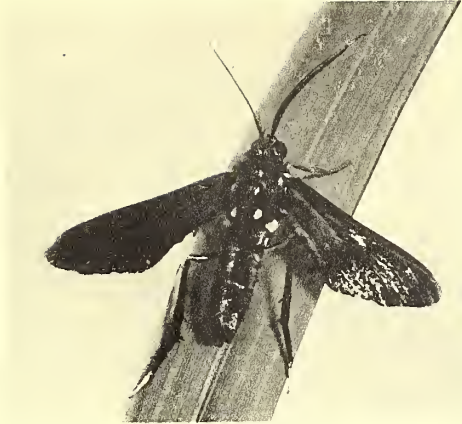


FIG. 15

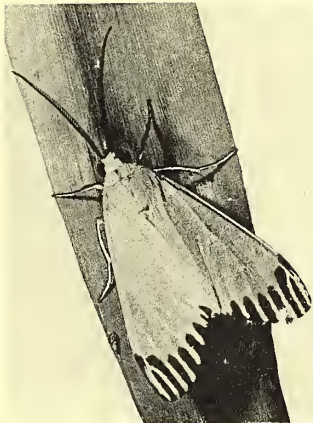


FIG. 16



FIG. 17



FIG. 18



FIG. 19

HABITS, PALATABILITY AND MIMICRY IN THIRTEEN CTENUCHID MOTH SPECIES FROM TRINIDAD, B.W.I.

Serological Relationships among Members of the Order Carnivora¹

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THE serological technic has been used in taxonomic studies for more than fifty years. The discovery of precipitins by Krause in 1897 and the publication in 1904 of Nuttall's book applying the new technic to problems of animal relationships gave taxonomists an approach which showed great promise of clarifying disputed or undetermined relationships. The precipitin technic has been used to a limited extent for the latter purpose, but has been quite extensively applied for verification of existing relationships based on morphological criteria.

The usefulness and trustworthiness of the technic have been shown by many workers. Studies have chiefly been made with vertebrates but there has also been research with a few of the invertebrate phyla. The following is a brief list of some representative papers in the field: Boyden (1926, 1934, 1943), Boyden & Noble (1933), Wolfe (1936), Brown & Heffron (1928), Eisenbrandt (1938), Wilhelmi (1940), Martin & Cotner (1934), Baier & Wolfe (1942), Gemeroy (1943) and Leone & Pryor (1954). It seems to us that the greatest value of the serological technic now lies in its possibility of settling questionable animal or plant relationships.

Perhaps no other order of the Class Mammalia contains such a diversified group of animals as does the Order Carnivora. This diversity has been responsible for considerable conflict and uncertainty in attempts at classification. The problem lies not so much in the over-all picture of Carnivora classification as in the grouping of related forms in the suborders and superfamilies. Most authors seem to agree that the order should

be divided into two suborders: the Fissipedia and the Pinnipedia. There are disagreements as to the relationships and inter-relationships among the families of the Fissipedia and the relationships of these families to the Pinnipedia. Winge (1923-24) and Scott (1937) both seem to favor combining the Ursidae, Canidae and Procyonidae into one group, with the Mustelidae as a distinct but associated family, and the Viverridae and Hyaenidae into another group, with the Felidae as a distinct but associated family. Winge associates the Pinnipedia with the Ursidae and Canidae. Beddard (1902), Romer (1933) and Simpson (1945) favor combining the Canidae, Ursidae, Procyonidae and Mustelidae into one superfamily and the Viverridae, Hyaenidae and Felidae into another superfamily. Beddard apparently believes the Pinnipedia closely associated with the Mustelidae, whereas Romer seems to indicate that the Pinnipedia are most closely associated with the Ursidae and Canidae. Other authors have opinions varying slightly from the above.

Since their discovery in the late Nineteenth Century, little use has been made of serological reactions in the taxonomic study of the Carnivora. Nuttall (1904) summarized the results of his flocculation tests with the sera of 56 different species of Carnivora. In general his results agreed with the systematic position of the species tested. With this lone exception no other extensive work has been done on the serological taxonomy of the Carnivora. Brief mention of them is made in several papers: Boyden (1926, 1942), Boyden & Gemeroy (1950) and Wolfe (1936).

An extraordinary study on the taxonomy of the Carnivora was included in the book by Reichert & Brown (1909) in which the relationships between various members were deter-

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mined by the resemblances and differences of hemoglobin crystals formed from the different species. On the basis of their study Reichert & Brown claimed that the Ursidae and Mustelidae showed a closer relationship to the Pinnipedia than did any of the other Fissipedia. A peculiar finding was that the hemoglobin crystals of the skunk more nearly resembled those of the Procyonidae, which in turn did not resemble those of the Pinnipedia. The hemoglobin crystals of the Canidae resembled those of the Pinnipedia less, while the crystals of the Felidae and Viverridae resembled those of the Pinnipedia least of all.

The classification and nomenclature used in this paper follow those of Simpson (1945) as much as possible.

MATERIALS AND PROCEDURES

Many of the blood sera used as antigens were received from the New York Zoological Park through the courtesy of Dr. L. J. Goss and from the San Diego Zoo and the Serological Museum of Rutgers University through the courtesy of Drs. C. R. Schroeder and Alan A. Boyden respectively. Table 1 presents a list of animals from which sera were obtained.

Both chickens and rabbits were used for the production of antisera. Three different technics of precipitin testing were employed. These were the ring (interfacial) test, the photorefractometer method of Libby (1938) and the microdensitometer method of Baier (1943). The latter two are turbidimetric methods; the photorefractometer measures scattered light produced by the flocculating particles and the microdensitometer measures transmitted light. The authors found it advisable to use different injection procedures in order to obtain antisera of different precipitating ability, for it was necessary to have quite heavy precipitates when the microdensitometer was used, and weaker precipitating sera when the photorefractometer was employed.

With one exception, all antisera used in the ring tests were produced in chickens. Each chicken was given a single intravenous inoculation of 1 ml. of a 2 per cent. solution of blood serum (the antigen). This injection procedure is the best for production of antiserum of low precipitating power, a high interfacial titer and good specificity (Wolfe, 1936). The birds were bled eight to ten days after the injection. The antisera were allowed to stand for at least seven days in the refrigerator before use, as *in vitro* changes occurred in the serum upon such standing (Wolfe, 1942). The one rabbit used was treated in the same manner

TABLE 1. ANIMALS USED IN STUDY

Order CARNIVORA

Suborder FISSIPEDIA

Family Canidae

- Canis familiaris* (dog)
- Canis lupus* (timber wolf)
- Vulpes fulva* (red fox)

Family Ursidae

- **Ursus americanus* (black bear)
- **Thalarcos maritimus* (polar bear)

Family Procyonidae

- Procyon lotor* (raccoon)
- ***Potos caudivolvulus* (kinkajou)
- ***Nasua narica* (coati-mundi)

Family Mustelidae

- Mustela furo* (ferret)
- Mephitis mephitis* (skunk)
- Taxidea taxus* (badger)
- Mustela vison* (mink)
- **Tayra* sp. (tayra)

Family Felidae

- **Felis concolor* (mountain lion)
- Felis domesticus* (house cat)
- Panthera pardus* (leopard)
- **Panthera tigris* (tiger)
- **Acinonyx jubatus* (cheetah)

Family Hyaenidae

- ***Hyaena hyaena* (striped hyaena)

Suborder PINNIPEDIA

Family Otariidae

- ****Eumetopias jubata* (Steller's sea lion)
- ****Zalophus californianus* (California sea lion)
- **Zalophus californianus* (California sea lion)

Family Odobenidae

- **Odobenus rosmarus* (walrus)

Family Phocidae

- ****Phoca vitulina richardii* (harbor seal)

Order ARTIODACTYLA

Family Bovidae

- Bos taurus* (cattle)
- Bison bison* (American bison)

Order PRIMATES

Family Hominidae

- Homo sapiens* (man)

*Sera furnished by Dr. L. J. Goss.

**Sera furnished by Dr. A. A. Boyden.

***Sera furnished by Dr. C. R. Schroeder.

All other sera collected from local sources, including Madison Zoo.

described for production of antisera used in the photonreflectometer method.

Both chickens and rabbits were used in the production of antisera for the photonreflectometer studies. The rabbits were given a single series of three intravenous injections on alternating days, totaling 3 ml. of undiluted serum; the first injection was 0.5 ml., the second 1 ml. and the third 1.5 ml. The chickens received the same number of injections and on similar days but the solution was a 2 per cent. solution of the antigen rather than undiluted serum. The rabbits and chickens were bled on the seventh day after the last injection.

The antisera used in the microdensitometer studies were produced in chickens and rabbits. The increased precipitating power of the antisera needed in such studies was produced by increasing the amount of antigen inoculated into the animals. The rabbits were given two more series of three injections each at an interval of approximately 30 days. Each series consisted of a total of 3 ml. of undiluted serum. The chickens were given only one injection series, totaling 3 cc. of undiluted serum in three injections. The rabbits and chickens were bled seven days after the last injection. It should be emphasized that the above injection procedures did not always result in antisera of sufficient potency, and rather than reinject the animals that were poor antibody producers they were discarded. Chickens were found to be much better producers of antibody than the rabbits.

The chickens and rabbits were starved for 18 to 24 hours before bleeding. The blood was removed by cardiac puncture and allowed to clot. The serum was removed after centrifugation and stored in the refrigerator.

The ring test was performed in a 1.8 per cent. saline solution when chicken antiserum was used and in a .9 per cent. buffered saline solution when rabbit antiserum was employed. Serial dilutions of the antigen were made from a 2 per cent. solution which in turn was made from the undiluted antigen. One-tenth of a milliliter of antisera was layered below the antigen solutions (.5 ml.). Readings were made at 5, 10, 20, 30 and 60 minutes, but only the 60-minute readings are recorded in this paper.

The test antigens employed in the photonreflectometer and microdensitometer studies were also serially prepared. The final reaction mixtures of antigen and antisera were approximately .9 per cent. for the rabbit system and 8 per cent. for the chicken system, since Goodman, Wolfe & Norton (1951) showed that 8 per cent. was the optimum for the chicken

antiserum system. In order to conserve antiserum, only alternate dilution tubes were used in the microdensitometer and photonreflectometer tests.

The photonreflectometer tests were conducted according to a procedure modified slightly from that outlined by Baier (1947). The cells used were standardized as to thickness. This means that the light beam passes through the same distance in the liquid of each set of cells. This is important in measuring the light-scattering effect of particles in a suspension. Comparative results cannot be obtained if this distance varies among the individual cells of each set. The microdensitometer tests were conducted according to the procedure outlined by Baier (1947). The tubes used in these tests were standardized according to diameter and transmission of light beams.

The photonreflectometer and microdensitometer tests were made with antigen dilutions so chosen that the final readings for the highest and lowest dilutions (antibody excess and antigen excess) equalled the control reading at those two points. This was not always possible at the antigen excess region because of the small amount of antigen that was available in several cases.

Values of the relationships are expressed in percentage. The homologous reaction is considered to be 100 per cent. and the heterologous reactions are related to this. The galvanometer readings were summated for all the antigen concentrations used when the photonreflectometer and microdensitometer technics were used.

RESULTS

Table 2 presents a summary of the results obtained with 15 different antisera using the ring test technic. The two anti-*Mustelidae* sera (anti-mink and anti-ferret) gave high cross-reactions not only with other mustelids but also with the dog, fox, black bear and raccoon. The degree of cross-reactions with members of the *Felidae* were considerably lower in two of the three tests made and the reactions with *Bovidae* and *Hominidae* were very low.

Only one *Canidae* antiserum was produced. The anti-red fox serum reactions indicated that the *Ursidae* and *Procyonidae* were more closely related to the *Canidae* than to the *Mustelidae* or *Felidae*.

The anti-black bear serum was a very specific serum and gave a high cross-reaction only with the raccoon serum. Much weaker reactions occurred with other families of *Fissipedia* and also with man,

TABLE 2. SEROLOGICAL RELATIONSHIPS AMONG THE CARNIVORA—RING TEST TECHNIC.
RELATIONSHIP VALUES EXPRESSED IN PER CENT.

Antigen Source	Antisera														
	Mink-67 (12800)*	Ferret-107 (51200)	Fox-165 (25600)	Black bear-162 (12800)	Cat-65 (51200)	Leopard-139 (25600)	Mountain lion-111 (25600)	Kinkajou-PC-10 (51200)	Coati-mundi-PC-10 (51200)	Raccoon-C-1416 (51200)	Steller's sea lion-C-155 (51200)	Steller's sea lion-C-163 (51200)	Walrus-PC-88 (6400)	Harbor seal-C-165 (25600)	Harbor seal** 12800
Suborder FISSIPEDIA															
Family Procyonidae															
Kinkajou								100			6.3				6.3
Coati-mundi									100						6.3
Raccoon	50	100	25	25		6.3	2.3	50	50	100	12.5	0	25	0	0
Family Ursidae															
Polar bear								12.5		50	6.3	12.5	25	0.4	
Black bear		100	25	100		3.1		6.3	100	50		6.3	25	0.8	
Family Canidae															
Red fox	50	25	100	1.6		0.4		12.5		25		0	25	0	
Dog	25	50	50	3.1	6.3	1.6	0.8								0
Family Mustelidae															
Ferret	100	100	12.5		4.7	1.6				25					
Skunk	50	50	3.1	3.1	12.5	3.1	0.4	6.3	12.5	50	12.5	1.6	12.5	0	
Mink	100	100		3.1		1.6	1.6								
Badger	50	50	3.1	3.1	3.1	3.1	1.6								
Family Felidae															
Cat	9.4	18.8	3.1	1.6	100	12.5	50			6.3					0
Leopard			3.1	3.1		100									
Mountain lion		25		6.3	100	50	100								
Suborder PINNIPEDIA															
Family Otariidae															
Steller's sea lion								50	100	25	100	100	50	3.1	25
Family Odobenidae															
Walrus								25	50	25	50		100	3.1	25
Family Phocidae															
Harbor seal								25	50			25	50	100	100
Order ARTIODACTYLA															
Cattle	6.3				3.1	0	1.2	0.8	3.1			0.8	0	0	
Bison	6.3	0	1.6		6.3	0									
Order PRIMATES															
Man	6.3	0.9	0.8	3.1	3.1		2.3								

* Ring test titer.

** Produced in rabbit; all others produced in chickens.

Three anti-Felidae sera were tested. All of these gave strong cross-reactions with the cat, leopard and mountain lion, but a low order of reactions with the members of other families. The intra-family results were very peculiar in one test. The reactions of the anti-leopard serum indicated that the leopard was more closely related to the mountain lion than to the house cat. Such unexpected results warrant further investigation.

The three Procyonidae sera were all quite aspecific in their cross-reactions. All these sera gave large reactions with the Pinnipedia and the anti-kinkajou serum indicated that these Pinnipedia were more closely related to the kinkajou than were the Mustelidae, Canidae and Ursidae. The one test made with a representative of the Felidae showed the cat to be more distantly related to the raccoon than to other Fissipedia.

TABLE 3. SEROLOGICAL RELATIONSHIPS AMONG THE CARNIVORA—MICRODENSITOMETER AND PHOTONREFLECTOMETER TECHNIQS. RELATIONSHIPS EXPRESSED IN PER CENT.

Microdensitometer						Photonreflectometer				
Antigen Source	Antisera	*Steller's sea lion-157	*Steller's sea lion-CU	Steller's sea lion-3698-3796	*Black bear-3659-3660	*Raccoon-CX	Steller's sea lion-5	*Wolf-PE	*Skunk-PB	*Cat-PA
Suborder FISSIPEDIA										
Family Procyonidae										
Kinkajou										
Raccoon		11.6	42 23.4	49.2	34.9	65.7 100	18.2	16.7	0	1.37 0.7
Family Ursidae										
Polar bear		34.9	39	55.6	93	53.6	15.7	21.6	15.9	0
Black bear		26.7	35.9	59.5	100	26.9	18.4	18.8	11.2	22
Family Canidae										
Red fox		20.5	13.4	47.3	38.4	18.6		52.5		0
Dog							2.9	88.1		0
Timber wolf								100	5.	1.3
Family Mustelidae										
Skunk			30.7	55.3	45.3	37.3	20.1		100	2
Ferret							13.1	12.1	11.3	1
Tayra									15.1	
Family Felidae										
Cat							6.1	1	3.2	100
Tiger							0			50.4
Mountain lion										47.8
Cheetah										76.6
Family Hyaenidae										
Hyaena									0	18.3
Suborder PINNIPEDIA										
Family Otariidae										
Steller's sea lion		100	100	100	45.3	32.7	100	9.3	6	0
Cal. sea lion							82.6			.9
Family Odobenidae										
Walrus							45.5	8.9	8.1	
Family Phocidae										
Harbor seal		81.5	52.4	76.6	44.2		47.4	9	10.3	
Order ARTIODACTYLA										
Cattle			14.4	17.7	5.2	4.5				

* Antisera produced in chickens; other produced in rabbits.

Five anti-Pinnipedia sera were tested. They all gave distinct suborder reactions. One of the two anti-sea lion sera was more specific than the other and its reactions indicated that the Ursidae were more closely related to the sea lion than was the raccoon, fox or skunk. The anti-walrus sera was aspecific; it gave fairly dis-

tinct subordinal reactions but the degree of reactions with representatives of the Fissipedia showed a similarity of the relationships of all four families of this suborder to the Pinnipedia. The reactions of the two harbor seal antisera were interesting. The antiserum (C-165) produced in the chicken was highly specific and its

reactions with the blood of the sea lion and walrus were very low. It gave no reactions with the raccoon, fox or cat and only slight reactions with the polar bear and black bear. On the other hand, the antiserum produced in the rabbit gave reactions with the kinkajou and coati-mundi but not with the raccoon, dog or cat. No explanation suggests itself for the differences shown by these two antisera.

Table 3 records the results secured with the turbidimetric technic. Nine antisera were used and of these four were produced against the sea lion. These four antisera gave definite subordinal reactions and the three that were tested by the microdensitometer method indicated that the Ursidae were probably more closely related to the Pinnipedia than were the red fox or raccoon. On the other hand reactions with antiserum-CU were slightly higher for the kinkajou than with the Ursidae and antiserum 3698-3796 gave reactions with the skunk sera that were of similar magnitude to that of the Ursidae.

The black bear antiserum gave distinct familial reactions and the cross-reactions with the Pinnipedia were slightly higher than with the raccoon, red fox and skunk. The high degree of cross-reaction with the polar bear could indicate that a closer relationship exists than the present classification of these animals indicates. It would be unsafe to argue this question on the evidence of but one antiserum.

The anti-raccoon serum results showed the expected close relationship between the raccoon and the kinkajou. The Ursidae, Mustelidae and Pinnipedia showed a closer relationship to the Procyonidae than did the Canidae. In this particular series of tests the great difference between the polar bear result and the black bear result is strange considering the close relationship shown between these two animals in other tests. The authors cannot account for this variation but future tests may give a satisfactory answer.

The anti-wolf serum results gave an excellent example of intra-family relationships. The dog showed an 88 per cent. relationship to the wolf, while the red fox showed only a 52 per cent. relationship. Of the families tested, the Ursidae and Procyonidae seemed to be more closely related to the Canidae than were the mustelids. The representatives of three families of Pinnipedia showed a remarkably similar relationship to the wolf, while the cat (Felidae) was most distantly related.

The anti-skunk serum had relatively low precipitating power and was highly specific. The ferret and the tayra are members of the subfamily Mustelinae while the skunk belongs to the subfamily Mephitinae. The ferret and tayra

showed no closer relationship to the skunk than did the Ursidae. The Pinnipedia, Canidae and Felidae showed distant relationship while the raccoon and hyaena gave no cross-reactions.

The anti-cat serum results showed strong intra-family relationships but extremely weak inter-family relationships with all but the Hyaenidae. The intra-family results were peculiar. The cheetah showed a 76 per cent. relationship to the house cat while the tiger showed a 50 per cent. relationship and the mountain lion showed a 47 per cent. relationship. From these limited data one gets the impression that the tiger and mountain lion might belong to a different genus than the house cat. These results warrant much more research.

DISCUSSION

The findings set forth above are at least a beginning in the serological study of the relationship of the Carnivora. The species used in the study were chosen primarily because of their availability.

As indicated previously, authorities disagree about the relationship of the families of the Fissipedia to each other and to the Pinnipedia on the basis of comparative anatomy and paleontology. This has resulted in great variations and confusion in the classification and nomenclature of the Order Carnivora. On the basis of the serological data presented in this study, the following tentative conclusions can be drawn:

1. The Pinnipedia are more closely related to the Ursidae, Canidae, Mustelidae and Procyonidae than to the Felidae and Hyaenidae.
2. The closest serological resemblance exists between the Ursidae and Pinnipedia.
3. The Felidae and Hyaenidae are more closely related to each other than to any other family.
4. The polar bear seems to be quite closely related to the black bear and possibly should be included in the same genus.

If additional data support present findings, it might mean that the nomenclature of members of the family Felidae should be revised. Simpson in his work on the classification of mammals came to this same conclusion in his discussion of the taxonomy of the Felidae.

To attempt a serological classification of the Carnivora on the basis of the results presented in this paper might be premature. However, certain indications are given by these somewhat limited data. The tendency to classify the Canidae, Ursidae, Procyonidae and Mustelidae together into one superfamily (Canoidea) is perfectly valid serologically. Whether the Felidae,

Hyaenidae and Viverridae can be classified together into another superfamily serologically will have to be determined in the future. There are very strong indications that the suborders Fissipedia and Pinnipedia do not exist serologically. Future research may show that there are three or even four serological suborders of the Carnivora.

The authors realize the shortcomings of this paper as well as other serological research in which animal relationships have been considered. The shortcomings are due to the lack of materials to make more complete studies. It would be much more preferable to concentrate on fewer species but with larger numbers of specimens so that a number of antisera could be produced against each species and tested against several members of each studied. In this way it might be possible to make a statistical analysis of the data and one that might yield significant results rather than mere indications.

SUMMARY

1. Serological tests were carried out using the blood sera of 23 different species from nine families of the Order Carnivora, two sera of the Order Artiodactyla, and human serum (Order Primates).

2. The ring test, the Baier microdensitometer and the Libby photonreflectometer were all used in performing these tests.

3. Where comparable reactions were made, the results of the microdensitometer and photonreflectometer tests paralleled those of the ring test.

4. A serological basis for the classification of the Carnivora was indicated.

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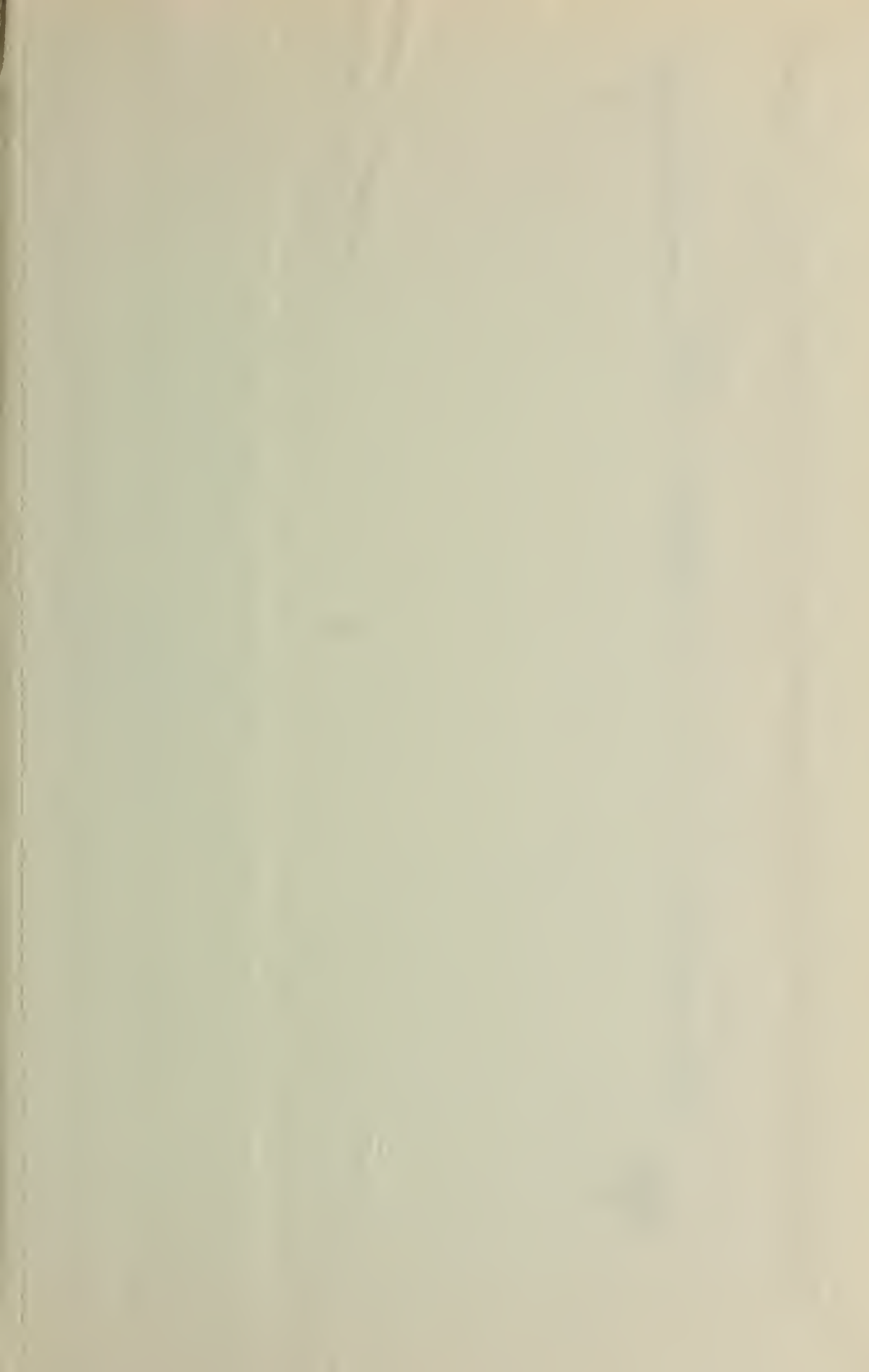
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